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Research Article

Fungi associated with seagrass *Enhalus acoroides* in Puttalam Lagoon, Sri Lanka: Discovery of two new species (*Neodevriesia zeylanica* and *Neooccultibambusa zeylanica* (*Dothideomycetes*)) and taxonomic validation of *Halophilomyces* (*Sordariomycetes*)

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Abstract

During our ongoing research on seagrass-associated fungi in Kalpitiya, Puttalam Lagoon, Sri Lanka, ten endophytic fungal strains have been isolated from healthy leaves, roots, and rhizomes of *Enhalus acoroides*. A surface sterilization method was used for the isolation of fungi. Pure cultures obtained were induced to sporulate. Phylogenetic analyses based on multi-gene regions (ITS, LSU, SSU, *rpb*2, and *tef*1-*α*) were carried out for species identification. *Neodevriesia zeylanica* Wijayaw. et al. and *Neooccultibambusa zeylanica* Wijayaw. et al. are introduced as novel species, along with two new country and host records, i.e., *Neodevriesia saximollicula* D.S.Paiva and *Thalassodendromyces purpureus* Vohník & Réblová. Two strains have been confirmed as *Halophilomyces hongkongensis* Xiao Wang et al. (nom. invalid), the type species of *Halophilomyces* Xiao Wang et al. (nom. invalid). *Halophilomyces hongkongensis* (based on the newly isolated strains) has been validated and provided with a new name, *Halophilomyces zeylanica* Wijayaw. et al., along with the designation of a new holotype and ex-type, respectively.

Key words: Endophytes, marine fungi, new records, phylogeny, taxonomy

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Introduction

Fungi are ubiquitous microorganisms found in a variety of environments, often quite challenging for life (Gostinčar et al. 2023). Marine habitats provide important niches for different groups of fungi and fungus-like taxa (Wijayawardene et al. 2022) and are currently reported to harbor ca. 2,253 species (https://www.marinefungi.org/ *fide* Jones et al. 2019; accession date 11 November 2025).

Given this situation, fungi from different marine substrates, such as algae, seaweed, seagrasses, and marine sponges, have been characterized both taxonomically and biochemically. On a global scale, many studies are available on seagrass-inhabiting fungal endophytes (e.g., Panno et al. 2013). Rajakaruna et al. (2024) discussed the importance of exploring seagrass-associated fungi, especially in understudied geographical regions, which can be rich in novel taxa that are useful in the pharmaceutical industry. To the best of our knowledge, no previous studies have been conducted in Sri Lanka, a biodiversity-rich country with the potential for high fungal diversity but an understudied geographic location. Since Sri Lanka belongs to the Indo-Pacific bioregion and is considered a biodiversity hotspot, investigating seagrass-associated fungi has the potential to discover new fungi with useful bioactivities.

In this study, we collected *Enhalus acoroides* (Linnaeus f.) Royle, 1839 samples from three sampling sites in shallow coastal waters of nearby localities near Kalpitiya, Puttalam Lagoon, Sri Lanka. Ten endophytic fungal strains have been isolated from healthy leaves, roots, and rhizomes using the surface sterilization method. According to the BLAST results of ITS sequence data, these strains belong to four different genera: viz., *Neodevriesia* (in *Neodevriesiaceae*, *Mycosphaerellales*) and *Neooccultibambusa* (in *Occultibambusaceae*, *Pleosporales*) in the class *Dothideomycetes*, and *Thalassodendromyces* (in *Lulworthiaceae*, *Lulworthiales*) and *Halophilomyces* (in *Lulworthiaceae*, *Lulworthiales*) in the class *Sordariomycetes*. Based on multi-locus phylogenetic analyses, we introduce two new species, i.e., *Neodevriesia zeylanica* Wijayaw. et al. and *Neooccultibambusa zeylanica* Wijayaw. et al., and two new country and host records (i.e., *Neodevriesia saximollicula* D.S. Paiva and *Thalassodendromyces purpureus* Vohník & Réblová).

Furthermore, two strains are confirmed as *Halophilomyces hongkongensis* Xiao Wang et al., the type species of *Halophilomyces* Xiao Wang et al. (Wang et al. 2024). However, *Halophilomyces hongkongensis* is invalidly published (Art. 40.7), and, being the type, *Halophilomyces* is also invalid. In this study, we validate *Halophilomyces hongkongensis* (based on the newly isolated strains) by providing a new name, *Halophilomyces zeylanica* Wijayaw. et al., and designating a new holotype and ex-type.

Materials and methods

Sample collection

The *Enhalus acoroides* (L.f.) Royle seagrass plants were collected on two occasions during low tide (23 August and 26 October 2023) from three sampling sites in shallow coastal waters of Puttalam Lagoon (8°08'38.80"N, 79°44'11.86"E; 8°13'09.90"N, 79°45'01.63"E; and 8°14'52.83"N, 79°46'17.80"E).

The sampling sites were separated by an average distance of approximately 8.2 km. *Enhalus acoroides* was identified at the sampling site by its unique, long, ribbon-like leaves; rhizomes covered with fibrous bristles; and cord-like roots (Fig. 1). Three whole plants were collected from each sampling site. All plants were manually uprooted while snorkeling. The collected plants were washed thoroughly at the respective sampling site with seawater to remove debris and brought to the laboratory in plastic containers along with seawater. The lids of the containers were kept open, and the plants were maintained in submerged conditions until processing.

Fungal isolation

In the laboratory, the leaves, roots, and rhizomes of undamaged plants from each sampling site were separated and washed thoroughly with seawater. Before surface sterilization, the tissues were cut into manageable segments. For leaf segments, surface sterilization was carried out according to Devarajan et al. (2002) and Venkatachalam et al. (2015) by rinsing with 70% ethanol for 5 s, immersing in 4% sodium hypochlorite for 60 s, and rinsing with sterile distilled water. Due to the higher microbial load and surface contaminants associated with underground tissues, a modified sterilization protocol was applied for roots and rhizomes, involving rinsing with 70% ethanol for 15 s, immersion in 4% sodium hypochlorite for 60 s, followed by rinsing with sterile distilled water. After surface sterilization, the tissue segments were blotted dry using sterile filter paper. An imprint of each tissue segment was made on the surface of the Potato Dextrose Agar (PDA) plate to verify the efficacy of the surface sterilization protocol. Following the imprint, the edges of each segment were trimmed, and the remaining tissue was divided into six segments. These were plated on 9 cm diameter PDA plates amended with ciprofloxacin (150 mgL^{-1}). Another set of tissue segments, similarly surface-sterilized, was plated on PDA prepared using undiluted seawater (filtered through Whatman No. 1 filter paper) collected from the same lagoon.

Cultures were incubated for 45 days at room temperature (29 °C). The culture plates were monitored periodically, and the endophytic fungi growing out from the tissue segments were subcultured onto fresh PDA medium. All resulting isolates were purified using the hyphal tip purification technique (Senanayake et al. 2020). Each isolate was assigned a unique code corresponding to its host tissue (leaf, root, or rhizome), sampling site, and the specific isolation medium used (standard PDA or seawater PDA). Pure cultures were maintained for further morphological and molecular characterization.

Morphological characterization

Mycelial plugs (6 mm) from 7-day-old cultures grown on PDA were transferred to new plates containing PDA, Malt Extract Agar (MEA), PDA prepared using seawater, and *Enhalus acoroides*-infused medium. The cultures were incubated for 14 days at 25 °C (±1 °C). At the end of the incubation period, photographs of colonies were taken using a Canon EOS REBEL T7 (Canon Inc., Tokyo, Japan). To determine the growth rate, radial growth measurements were taken by averaging the two perpendicular diameters for each colony (Hendricks et al. 2017).

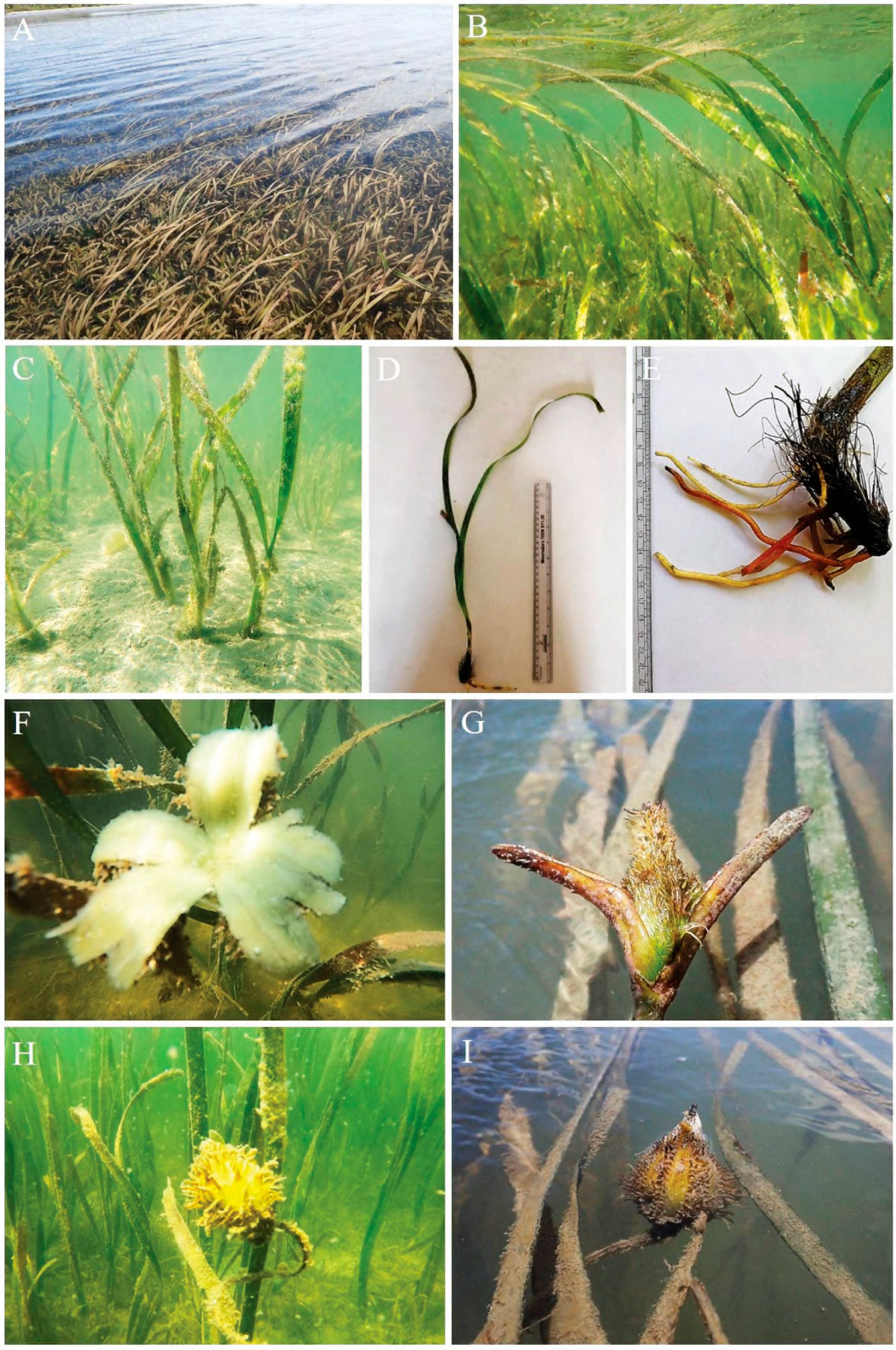

Figure 1. Morphological and reproductive features of *Enhalus acoroides*. **A–C.** Growth habit and submerged canopy in the natural habitat; **D.** Complete shoot with scale; **E.** Rhizome showing persistent black fibers and roots; **F.** Opened fruit; **G.** Female flower; **H–I.** Mature bristly fruit.

The colony characteristics, including color, form, margin, elevation, zonation, and sporulation, were recorded for each medium type.

Slide cultures were prepared to observe microscopic features. The microscopic features of fungal isolates were observed under a Nikon ECLIPSE Ci upright microscope (Nikon, Tokyo, Japan) and a Nikon SMZ18 stereomicroscope (Nikon, Tokyo, Japan), and measurements of microscopic features were made using ImageJ software. At least 30 measurements were taken for each microscopic structure. The illustrated figures were processed using Adobe Photoshop CS6 software (Adobe Systems, San Jose, CA, USA).

Techniques used for sporulation of cultures

To induce sporulation in the fungal isolates, several nutritional and environmental methods were employed. Nutritional stress was applied by subculturing isolates onto half-strength media, specifically 1/2 Potato Dextrose Agar (PDA) and 1/2 Soya-Wheat Agar (SW). To simulate host-specific conditions, *E. acoroides* tissue extract was incorporated into the media, and sterilized *E. acoroides* tissue segments were embedded in the agar to serve as a natural lignocellulosic scaffold. Mechanical stimulation was provided via the toothpick method to facilitate mycelial attachment and development of fruiting bodies. Physical stressors included a cold shock treatment at 4 °C for 24 hours and ultraviolet (UV) irradiation for 5 seconds. All cultures were subsequently incubated under a standard 12-hour light/dark cycle and monitored for the development of reproductive structures.

Herbarium specimens (including dried cultures) and living culture depositions

Newly generated cultures were deposited in the culture collection of the University of Colombo (**UOCCC**) and the Rajarata University Fungal Culture Collection (**RUFCC**). Dried cultures were deposited as herbarium specimens in the Rajarata University Fungarium (**RUSLH**).

Registration of novel taxa

Index Fungorum Registration Identifiers were obtained for the new species and newly validated species, as mentioned in Index Fungorum (2025).

Fungal genomic DNA extraction, PCR amplification, and sequencing

Fresh mycelia were scraped from fungal cultures grown on PDA and transferred into 1.5 mL microcentrifuge tubes. DNA extraction followed a laboratory-developed protocol based on Al-Samarrai and Schmid (2000). Fungal cultures were grown in Potato Dextrose Broth (PDB) at 28 °C for 7 days. The mycelia were harvested by centrifugation to remove excess liquid and homogenized in 500 µL of preheated SDS-containing extraction buffer, followed by incubation at 65 °C. DNA was purified using potassium acetate and chloroform:isoamyl alcohol (24:1) and precipitated with ice-cold isopropanol. The resulting DNA pellets were washed with 70% ethanol,

resuspended in TE buffer, and stored at −20 °C. DNA quality and concentration were assessed using 1% agarose gel electrophoresis and a NanoDrop 1000 spectrophotometer. Polymerase chain reaction (PCR) amplifications were performed using the following primer pairs: ITS1F/ITS4 for the internal transcribed spacer region (ITS, including 5.8S rDNA); NS1/NS4 for the nuclear ribosomal small subunit (SSU, 18S rDNA) (White et al. 1990; Gardes and Bruns 1993); and LR0R/LR5 for the nuclear ribosomal large subunit (LSU, 28S rDNA) (Vilgalys and Hester 1990).

The reaction was performed in a final volume of 25 µL DNA template containing 12.5 µL of 2 × GoTaq Green Master Mix (Promega, USA), 2.5 µL of each primer (10 µM), 5.5 µL of nuclease-free water, and 2 µL of genomic DNA template (50 ng/µL). PCR amplifications were carried out using the T100 Thermal Cycler (Bio-Rad, USA) with an initial denaturation step at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 1 min, annealing for 1 min, and extension at 72 °C for 1 min, with a final extension at 72 °C for 10 min. The annealing temperatures were optimized for each gene locus as follows: ITS, 48 °C; LSU, 48 °C; and SSU, 55 °C. All products were visualized by agarose gel electrophoresis (1% gel, 100 V, 30 min) stained with ethidium bromide. The PCR products were sequenced at Genelabs Medical, Sri Jayawardenepura Kotte, Sri Lanka, and Macrogen Inc., South Korea.

Phylogenetic analyses

Forward and reverse sequences of the newly generated isolates were assembled using BioEdit (Hall 2004). The resulting consensus sequences were submitted to the NCBI database for BLAST searches to identify the closest taxonomic relatives (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch). Additional sequences for the phylogenetic analyses in this study were obtained from recent literature and downloaded from GenBank (https://www.ncbi.nlm.nih.gov/WebSub/?form=history&tool=-genbank). The single-gene sequences were aligned using MAFFT v. 7 (Katoh and Standley 2013) (https://mafft.cbrc.jp/alignment/server), and ambiguous sites were trimmed using trimAl v.1.2rev59 (Capella-Gutiérrez et al. 2009). Subsequently, the trimmed single-gene alignments were merged into a single FASTA file using Matrix 1.9 (Vaidya et al. 2011). Finally, the FASTA format was converted to PHYLIP and NEXUS formats using AliView for the maximum likelihood (ML) and Bayesian inference (BI) analyses, respectively.

Maximum likelihood (ML) analysis was performed using RAxML-HPC2 on XSEDE (v. 8.2.12) via the CIPRES Science Gateway v. 3.3 (http://www.phylo.org/portal2), using the GTRGAMMA substitution model with 1,000 bootstrap replicates (Stamatakis et al. 2008; Stamatakis 2014). Bayesian analyses were conducted using MrBayes 3.2.7a, and the best model for each dataset was evaluated using MrMTgui (Ronquist et al. 2012; Ma 2016). Six simultaneous Markov chains were run for 1 million generations, and trees were sampled every 100th generation. The final trees were visualized in FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) (Rambaut 2012) and formatted using Adobe Illustrator CS v. 5. All newly generated sequences were deposited in GenBank, and the sequence alignments and phylogenetic trees were deposited in TreeBASE (Tables 1–4).

Table 1. Taxa used in the phylogenetic analyses of *Neodevriesia s. str.* and their corresponding strain numbers and GenBank accession numbers. The newly generated sequences are in bold. Type strains or type specimens are labeled with "ᵀ"; "NA" indicates no available sequences.

Species name	Strain/voucher no.	GenBank accession number		
		ITS	LSU	*rpb2*
Neodevriesia aestuarina	MUM 19.27ᵀ	MN046879	MN653390	NA
N. agapanthi	CPC 19833ᵀ	NR_111766	NG_042688	KJ564346
N. bulbillosa	CBS 118285ᵀ	AY559341	KF310029	KF310102
N. capensis	CBS 130602ᵀ	JN712501	JN712569	NA
N. infestans	OUCMBI110119ᵀ	KU578112	KU578114	KY415955
N. infestans	OUCMBI101247	KU578115	KU578117	KY415956
N. coccolobae	CBS 145064ᵀ	MK047432	MK047483	NA
N. coryneliae	CPC 23534ᵀ	NR_132905	KJ869211	NA
N. cycadicola	CBS 145553ᵀ	NR_165568	NG_067886	NA
N. fici	LWHHK-7ᵀ	JX294932	NA	NA
N. fraserae	CBS 128217ᵀ	NR_144961	NA	NA
N. grateloupiae	OUCMBI101249ᵀ	KU578118	KU578120	KY415957
N. grateloupiae	OUCMBI141254	KX237686	KX237688	KY415958
N. hilliana	CPC 15382ᵀ	GU214633	GU214414	NA
N. imbrexigena	CAP1371	JX915745	JX915749	NA
N. kalakoutskii	CBS 148320 ᵀ	NR_177163	NA	NA
N. knoxdaviesii	CBS 122898ᵀ	EU707865	EU707865	NA
N. lagerstroemiae	CPC 14403ᵀ	GU214634	GU214415	KF902233
N. longicatenispora	FMR 18825ᵀ	NR_198696	NG_243975	NA
N. manglicola	NFCCI 4382	MN061371	MN061356	NA
N. maravalensis	CBS 48137T	PV664939	PV664965	NA
N. metrosideri	CBS 145084ᵀ	MK047450	MK047500	NA
N. modesta	CCFEE 5672ᵀ	KF309984	KF310026	KF310093
N. oceanoplastica	SFC20250301-M047ᵀ	PX062434	PX091334	PX071816
N. pakbiae	CPC 25044ᵀ	NR_137997	KR476775	NA
N. poagena	CPC 25086ᵀ	KR611885	KR611903	NA
N. queenslandica	CBS 129527ᵀ	JF951148	KF901839	KF902234
N. sardiniae	CCFEE 6202ᵀ	KP791765	KR781052	KT247887
N. saximollicula	PL127	PP151470	PP151490	NA
N. saximollicula	**UOCCC 251201**	**PX788711**	**PX844596**	NA
N. saximollicula	**UOCCC 251209**	**PX957557**	**PX973408**	NA
N. scadoxi	CBS 149461ᵀ	NR_189519	OQ629056	OQ627940
N. sexualis	CBS 145568ᵀ	NR_165569	NG_067887	NA
N. shakazului	CPC 19782ᵀ	NR_111825	KC005797	KJ564347
N. simplex	CCFEE 5681ᵀ	KF309985	KF310027	KF310104
Neodevriesia sp.	CBS 118302	NA	GU323975	KF310100
N. stirlingiae	CPC 19948ᵀ	NR_120228	KC005799	NA
N. strelitziae	CBS 122379ᵀ	EU436763	GU301810	GU371738
N. strelitziicola	CBS 146019ᵀ	MN562144	MN567651	MN556812
N. tabebuiae	CBS 145065ᵀ	MK047433	MK047484	NA
N. xanthorrhoeae	CBS 128219ᵀ	HQ599605	HQ599606	NA
N. zeylanica	**UOCCC 251202ᵀ**	**PX796425**	**PX854882**	NA
N. zeylanica	**UOCCC 251210**	**PX973267**	**PX973446**	NA
Teratosphaeria complicata	CPC14535ᵀ	KF901781	KF902139	NA

Table 2. Taxa used in the phylogenetic analyses of *Neooccultibambusa s. str.* and their corresponding strain numbers and GenBank accession numbers. The newly generated sequences are in bold. Type strains or type specimens are labeled with "T"; "NA" indicates no available sequences.

Species name	Strain/voucher no.	GenBank accession number				
		ITS	LSU	SSU	*rpb2*	*tef1-α*
Brunneofusispora baoshanensis	ZHKUCC 23-0664T	OR636963	OR636973	OR646286	OR6457557	OR645755
B. baoshanensis	ZHKUCC 23-0665	OR636964	OR636974	OR646287	OR6457558	OR645756
B. clematidis	MFLUCC 17-2070T	MT310615	MT214570	MT226685	MT394692	MT394629
B. hyalina	MFLUCC 21-0008T	MW260330	MW287234	MW485613	MW512609	MW512606
B. inclinatiostiola	CGMCC 3.20403T	MZ964866	MZ964875	MZ964884	OK061075	OK061069
B. inclinatiostiola	GZCC 21-0185	MZ964867	MZ964876	MZ964885	OK061076	OK061070
B. kevinimucosa	CGMCC 3.28689T	PQ773399	PQ773419	NA	NA	PV059181
B. mahoniae	GUCC 24-0060T	PQ215686	PQ215696	PQ215692	PQ226183	PQ226179
B. sennae-torae	BRIP 72515d	OK493236	OK493235	NA	NA	NA
B. sinensis	KUMCC 17-0030T	MH393558	MH393557	MH393556	NA	MH395329
B. sinensis	MFLUCC 20-0016	MT159630	MT159624	MT159636	MT159613	MT159607
Brunneofusispora sp.	X135	MK304223	NA	NA	NA	NA
Neooccultibambusa chiangraiensis	MFLUCC 12-0559T	KU712442	KU764699	KU712458	NA	KU872761
N. coffeae	KUNCC 24-18351T	OR428394	OR428416	OR428374	OR515518	OR509748
N. coffeae	KUNCC 24-18353	OR428393	OR428415	OR428373	OR515517	OR509747
N. jonesii	MFLUCC 16-0643	NA	KY111437	KY111438	NA	NA
N. kaiyangensis	CGMCC 3.20404T	MZ964868	MZ964877	MZ964886	OK061077	OK061071
N. kaiyangensis	GZCC 21-0184	MZ964869	MZ964878	MZ964887	OK061078	OK061072
N. pandanicola	KUMCC 17-0179T	MG298941	MG298940	MG298942	MG298944	MG298943
N. thailandensis	MFLUCC 16-0274T	MH275074	MH260308	MH260348	MH412758	MH412780
N. trachycarpi	CGMCC 3.20405	MZ964870	MZ964879	MZ964888	OK061079	OK061073
N. trachycarpi	GZCC 21-0181	MZ964871	MZ964880	MZ964889	OK061080	OK061074
N. zeylanica	**UOCCC 251208**	**PX861568**	**PX868941**	**PX868942**	NA	NA
N. zeylanica	**UOCCC 251214**	**PX975907**	**PX973467**	**PX973504**	NA	NA
N. zeylanica	**UOCCC 251207T**	**PX844579**	**PX868952**	**PX868972**	NA	NA
N. zeylanica	**UOCCC 251213**	**PX973270**	**PX975910**	**PX975911**	NA	NA
Neoroussoella clematidis	MFLUCC 17-2061T	MT310632	MT214587	MT226700	MT394701	MT394645
N. fulvicomae	MFLUCC 17-2073T	MT310633	MT214588	MT226701	MT394702	MT394646
Occultibambusa bambusae	MFLUCC 13-0855T	KU940123	KU863112	KU872116	KU940170	KU940193
O. chiangraiensis	MFLUCC 16-0380T	NA	KX655546	KX655551	KX655566	KX655561
O. fusispora	MFLUCC 11-0127T	KU940125	KU863114	NA	KU940172	KU940195
O. jonesii	GZCC 16-0117T	NA	KY628322	KY628324	KY814758	KY814756
O. kunmingensis	HKAS 102151T	MT627716	MN913733	MT864342	MT878453	MT954407
O. maolanensis	GZCC 16-0116T	NA	KY628323	KY628325	KY814759	KY814757
O. pustula	MFLUCC 11-0502T	KU940126	KU863115	KU872118	NA	NA
Ohleria modesta	CBS 141480	KX650563	KX650563	KX650513	KX650583	KX650534
Oh. modesta	MGC	KX650562	KX650562	NA	KX650582	KX650533
Roussoella nitidula	MFLUCC 11-0182T	KJ474835	KJ474843	NA	KJ474859	KJ474852
R. thailandica	MFLUCC 11-0621T	KJ474838	KJ474846	NA	NA	NA
Seriascoma didymosporum	MFLUCC 11-0179T	KU940127	KU863116	KU872119	KU940173	KU940196
S. yunnanense	MFLU 19-0690T	NA	MN174695	MN174694	MN210324	MN381858
Thyridaria acaciae	CBS 138873T	KP004469	KP004497	NA	NA	NA
T. broussonetiae	CBS 141481T	KX650568	KX650568	KX650515	KX650586	KX650539
T. broussonetiae	TB	KX650567	KX650567	NA	KX650585	KX650538
T. broussonetiae	TB2	KX650570	KX650570	NA	KX650587	KX650540
Versicolorisporium triseptatum	JCM 14775T	AB365596	AB330081	AB524501	NA	NA

Table 3. Taxa used in the phylogenetic analyses of *Halophilomyces s. str.* and their corresponding strain numbers and GenBank accession numbers. The newly generated sequences are in bold. Type strains or type specimens are labeled with "T"; "NA" indicates no available sequences.

Species name	Strain/voucher no.	GenBank accession number		
		ITS	LSU	SSU
Achroceratosphaeria potamia	JF 08139	NA	GQ996538	GQ996541
Halazoon fuscus	NBRC105256	NA	GU252147	GU252148
H. fuscus	NBRC105256	NA	GU252147	GU252148
H. melhae	MF819^{T}	NA	GU252143	GU252144
H. purpurea	FCUL280207CF9	KT347218	JN886808	KT347202
H. purpurea	FCUL170907CP5	KT347219	JN886824	KT347201
Halophilomyces hongkongensis (= *H. zeylanica*)	HOMAR1	PP350734	PP347858	PP347844
H. hongkongensis (= *H. zeylanica*)	HOMAR2	PP350735	PP347859	PP347845
H. hongkongensis (= *H. zeylanica*)	HOMAR3	PP350736	PP347860	PP347846
H. hongkongensis (= *H. zeylanica*)	HOMAR4	PP350737	PP347861	PP347847
H. zeylanica	**UOCCC 251203^{T}**	**PX832229**	**PX860153**	**PX860155**
H. zeylanica	**UOCCC 251211**	**PX975908**	**PX975909**	**PX975912**
Lindriella thalassiae	AFTOL_ID_413	DQ491508	DQ470947	DQ470994
L. thalassiae	JK4322	NA	AF195633	AF195632
Lulwoana uniseptata	KMPB150	NA	AY878993	AY879036
Lu. uniseptata	KMPB82	NA	AY878994	AY879037
Matsusporium japonica	SUMCC H-08001^{T}	NA	OP646426	OP646428
Moromyces mangrovis	MFLUCC 17-0392^{T}	NA	OP884599	OP884603
M. varius	GR78	NA	EU848578	NA
Pisorisporium cymbiforme	PRM 924377	NA	KM588904	KM588901
Rambellisea gigliensis	HPa15	NA	OR369725	OR371482
R. gigliensis	HPa16	NA	OR371456	OR371483
R. halocynthiae	HPa50	NA	OR371457	OR371485
R. halocynthi	HPa51	NANA	OR371461	OR371484
Rostrupielladanica	TRä3137A^{T}	NA	DQ394094	NA
Ro. danica	BBH16759	NA	DQ394094	NA
Ro. longispora	JK4686	OP683566	OP683566	OP680781
Ro. longispora	TRä3137A	OP683566	OP683566	OP680781
Sammeyersia grandispora	NTOU3841	NA	KY026048	KY026044
S. grandispora	NTOU3847	NA	KY026049	KY026046

Results

Phylogenetic analysis

Multi-gene analyses for *Neodevriesia s. str.*

A phylogram was generated from an ML analysis of *Neodevriesia* based on combined ITS, LSU, and *rpb*2 sequence data of 43 taxa (including the new isolates), which comprised 2569 base pairs (ITS = 538, LSU = 858, and *rpb*2 = 1171) (TreeBASE Submission ID 32494) (The *rpb*2 locus was included to improve topology and resolution. A separate analysis of the ITS locus was performed to confirm the topology, which was similar to the multi-locus tree; the single-gene tree is provided as Suppl. material 1). The tree is rooted with *Teratosphaeria complicata* (CPC14535T). The best-scoring RAxML tree, with a final likelihood value of −12909.069600, is presented. The matrix contained 766

distinct alignment patterns with 46.42% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.242017, C = 0.256467, G = 0.288928, T = 0.212588; substitution rates: AC = 1.492415, AG = 1.850180, AT = 1.203640, CG = 1.238011, CT = 5.009471, GT = 1.000000; gamma distribution shape parameter α = 0.310960.

In the phylogenetic tree (Fig. 2), our two new strains (UOCCC 251201 and UOCCC 251209) formed a sister clade with *Neodevriesia saximollicula* (PL127, MUM 2348) with 100% ML and 1.00 BYPP statistical support. Moreover, two other new isolates (UOCCC 251202 and UOCCC 251210) formed a distinct lineage to *Neodevriesia shakazului* (CPC 19782) with high statistical support (92% ML and 0.99 BYPP).

Table 4. Taxa used in the phylogenetic analyses of *Thalassodendromyces s. str.* and their corresponding strain numbers and GenBank accession numbers. The newly generated sequences are in bold. Type strains or type specimens are labeled with "ᵀ"; "NA" indicates no available sequences.

Species name	Strain/Voucher No.	GenBank accession number		
		ITS	LSU	SSU
Achroceratosphaeria potamia	CBS 125414ᵀ	MH863679	GQ996538	GQ996541
Cumulospora marina	MF46	NA	GU252135	GU252136
Halazoon fuscus	NBRC 105256	NA	GU252147	GU252148
H. melhae	MF819ᵀ	NA	GU252143	GU252144
Halomyrma pluriseptata	CCF 3788ᵀ	PV441105	PV441119	PV441112
Halo. pluriseptata	CCF 3787	PV441106	PV441120	PV441113
Halophilomyces hongkongensis	HOMAR2ᵀ	PP350735	PP347859	PP347845
Hydea pygmea	NBRC 33069	NA	GU252133	GU252134
Lindra crassa	ATCC 56663ᵀ	NA	NA	AY878999
Matsusporium tropicale	NBRC 32499	NA	GU252141	GU252142
Moleospora maritima	MF 836ᵀ	NA	GU252137	GU252138
Moromyces varius	GR78	NA	EU848578	EU848593
Paralulworthia candida	MUT 5430ᵀ	MZ357724	MZ357746	MZ357767
P. elbensis	MUT 5422ᵀ	MZ357723	MZ357745	MZ357766
P. gigaspora	MUT 435ᵀ	MN649242	MN649250	MN649246
P. halima	CBS 208.64ᵀ	MH858421	MH870049	NA
P. mediterranea	MUT 5417ᵀ	MZ357721	MZ357743	MZ357764
P. posidoniae	MUT 5261ᵀ	MN649245	MN649253	MN649249
Rambellisea gigliensis	HPa3ᵀ	OR367423	OR369726	OR371466
R. halocynthiae	HPa50	OR367481	OR371457	OR371485
Rostrupiella danica	BBH 16759ᵀ	NA	DQ394094	NA
Sammeyersia grandispora	J.K. 4686	NA	DQ522856	DQ522855
Thalassodendromyces purpureus	CBS 153577ᵀ	PV441107	PV441121	PV441114
T. purpureus	CBS 153576	PV441108	PV441122	PV441115
T. purpureus	CBS 153646	PV441109	PV441123	PV441116
T. purpureus	CBS 153624	PV441110	PV441124	PV441117
T. purpureus	CBS 153625	PV441111	PV441125	PV441118
T. purpureus	**UOCCC 2512006**	**PX957527**	**PX854888**	NA
T. purpureus	**UOCCC 251212**	**PZ012345**	**PX973501**	NA
Zalerion maritima	FCUL280207CP1	KT347216	JN886806	KT347203
Z. maritima	NBRC 32137ᵀ	LC146746	LC146746	AY879031
Z. pseudomaritima	CMG 65ᵀ	MT235733	MT235750	MT235709

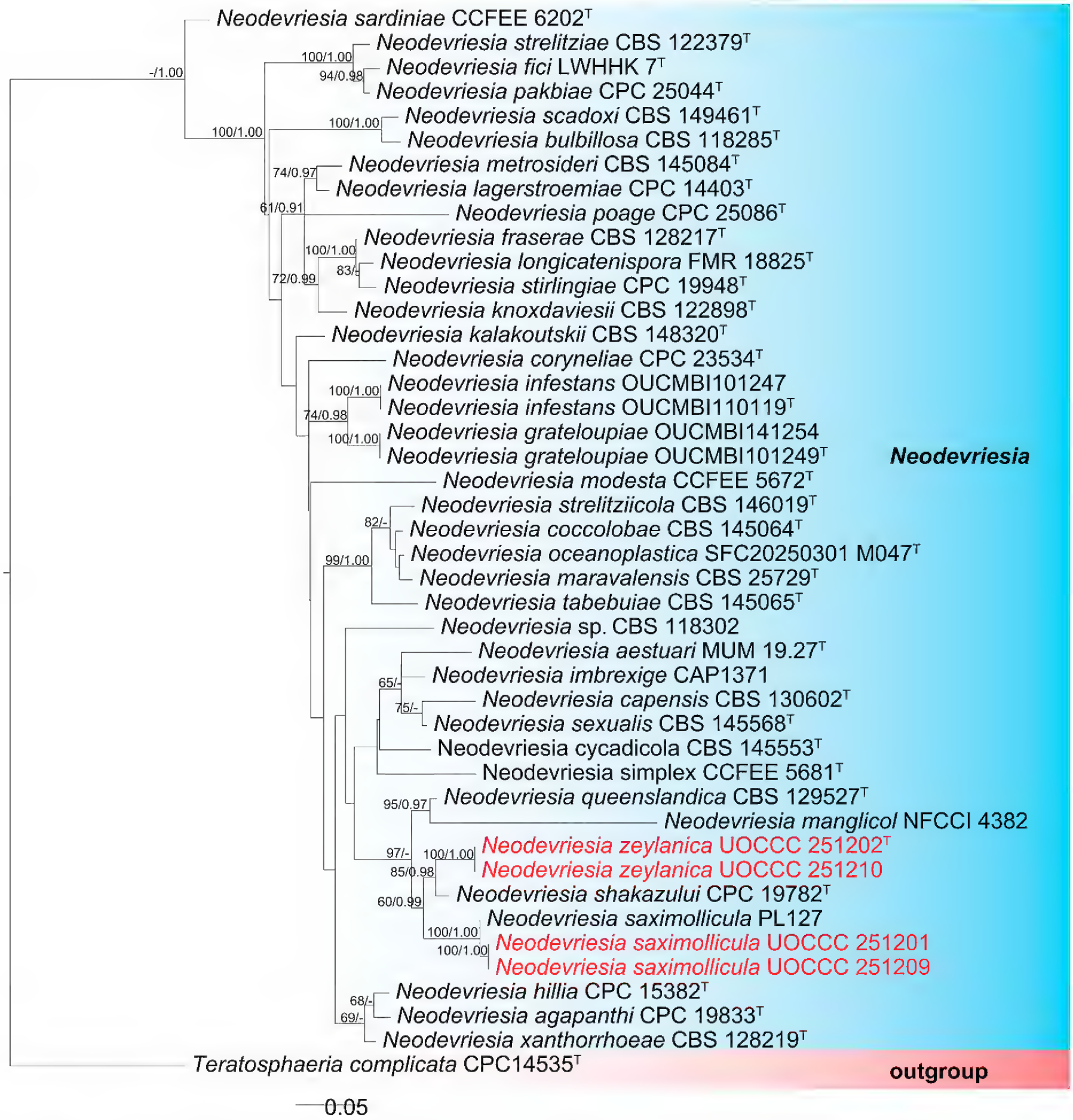

Figure 2. RAxML tree based on a combined dataset of partial ITS, LSU, and *rpb*2 DNA sequence analyses. Bootstrap support values for ML ≥ 60% and Bayesian posterior probabilities (BYPP) ≥ 0.9 are shown as ML/BI above the nodes. Type materials are indicated by the superscript "T" while newly generated sequences are shown in red.

Multi-gene analyses for *Neooccultibambusa s. str.*

A phylogram was generated from an ML analysis (using a concatenated dataset of ITS, LSU, SSU, *rpb*2, and *tef*1-*α* regions), which comprised 4374 characters with gaps (ITS = 531, LSU = 865, SSU = 1020, *rpb*2 = 1004, and *tef*1-*α* = 950) (TreeBASE Submission ID 32486) (The *tef*1-*α* locus was included to achieve better topology and resolution, following Hyde et al. (2018). A separate analysis of the ITS locus was carried out to confirm the topology, which was similar to the multi-locus tree. The single-gene tree is provided as Suppl. material 2). *Ohleria modesta* (CBS 141480, MGC) was used as the outgroup taxon. The best-scoring RAxML tree, with a final likelihood value of −24372.732742, is presented. The matrix had 1482 distinct alignment patterns, with 25.54% undetermined

characters or gaps. Estimated base frequencies were as follows: A = 0.246671, C = 0.252028, G = 0.270378, T = 0.230922; substitution rates: AC = 2.086124, AG = 5.211652, AT = 1.764318, CG = 1.722822, CT = 11.447364, GT = 1.000000; gamma distribution shape parameter α = 0.563581.

In the phylogenetic tree (Fig. 3), our new strains (UOCCC 251207, UOCCC 251213, UOCCC 251208, and UOCCC 251214) formed a sister clade with *Neooccultibambusa kaiyangensis* (CGMCC 3.20404 and GZCC 21-0184), *N. chiangraiensis* (MFLUCC 12-0559), and *N. coffeae* (KUNCC 24-18353 and KUNCC 2418351), with 75% ML value support.

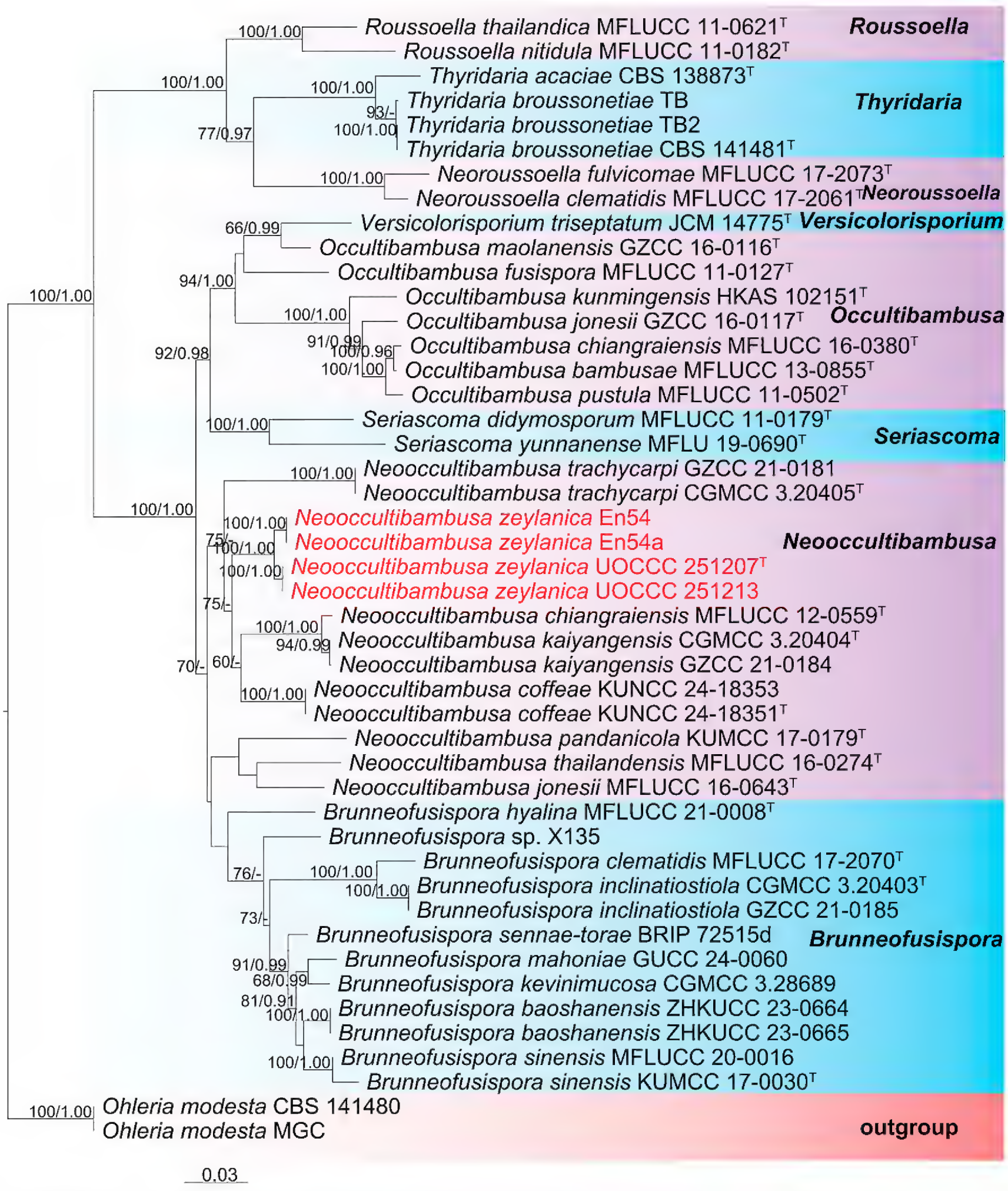

Figure 3. RAxML tree based on a combined dataset of partial ITS, LSU, SSU, *rpb*2, and *tef*1-*α* DNA sequence analyses. Bootstrap support values for ML ≥ 60% and Bayesian posterior probabilities (BYPP) ≥ 0.9 are shown as ML/BI above the nodes. Type materials are indicated by the superscript "T" while newly generated sequences are shown in red.

Multi-gene analyses for *Halophilomyces s. str.*

A phylogram was generated from an ML analysis based on combined ITS, LSU, and SSU sequence data of 37 taxa, which comprised 2457 base pairs (ITS = 534, LSU = 887, and SSU = 1034) (TreeBASE Submission ID 32493). The tree is rooted with *Achroceratosphaeria potamia* (JF 08139) and *Pisorisporium cymbiforme* (PRM 924377). The best-scoring RAxML tree, with a final likelihood value of −8938.534084, is presented. The matrix had 628 distinct alignment patterns, with 24.65% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.250520, C = 0.237936, G = 0.291273, T = 0.220271; substitution rates: AC = 1.442542, AG = 2.593080, AT = 0.854251, CG = 2.008941, CT = 6.565557, GT = 1.000000; gamma distribution shape parameter α = 0.678649.

In the phylogenetic tree (Fig. 4), the new strains (UOCCC 251203 and UOCCC 251211) clustered with *Halophilomyces hongkongensis* (HOMAR1, HOMAR2, HOMAR3, and HOMAR4) with 100% ML value support.

Multi-gene analyses for *Thalassodendromyces s. str.*

A phylogram was generated from an ML analysis (based on combined ITS, LSU, and SSU sequence data), and 35 strains were included in the sequence analysis, which comprised 3178 characters (ITS = 431, LSU = 879, and SSU = 1343; TreeBASE Submission ID 32490). *Achroceratosphaeria potamia* (CBS 125414) was used as the outgroup taxon. The tree topology of the ML analysis was similar to that of the BI analysis. The best-scoring RAxML tree, with a final likelihood value of −14387.797340, is presented. The matrix had 945 distinct alignment patterns, with 22.00% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.241245, C = 0.251235, G = 0.298972, and T = 0.208549; substitution rates: AC = 1.675090, AG = 2.751572, AT = 1.215209, CG = 1.798431, CT = 6.092003, and GT = 1.000000; gamma distribution shape parameter α = 0.736186.

In the phylogenetic tree (Fig. 5), two new isolates (UOCCC 2512006 and UOCCC 251212) clustered with *Thalassodendromyces purpureus* (CBS 153625, CBS 153577, CBS 153624, CBS 153576, and CBS 153646) with 100% ML and 1.00 BYPP value support.

Taxonomy

***Dothideomycetes* O.E. Erikss. & Winka**
***Mycosphaerellales* P.F. Cannon**
***Neodevriesiaceae* Quaedvl. & Crous**

***Neodevriesia* Quaedvl. & Crous, Persoonia 33: 24 (2014)**

Notes. The genus *Neodevriesia* was introduced by Quaedvlieg et al. (2014) to accommodate devriesia-like species that are phylogenetically distinct from *Devriesia s. str.* Currently, the genus comprises 36 species (Species Fungorum 2025; accessed 6 December 2025) and is reported from a broad range of habitats under different ecological conditions (e.g., **1)** *N. cladophorae* M.M.

Wang & W. Li from marine algae (*Cladophora* sp.) *fide* Wang et al. 2017; **2)** *N. queenslandica* (Crous, R.G. Shivas & McTaggart) Crous from leaves of *Scaevola taccada*), worldwide.

In this study, four strains of *Neodevriesia* were collected from *Enhalus acoroides*. Multi-locus phylogenetic analyses confirmed that two strains (UOCCC 251201 and UOCCC 251209) belong to *N. saximollicula* (Fig. 2). The other two strains formed a distinct lineage within *Neodevriesia s. str.* in our phylogenetic analysis; thus, we introduce *Neodevriesia zeylanica* Wijayaw. et al.

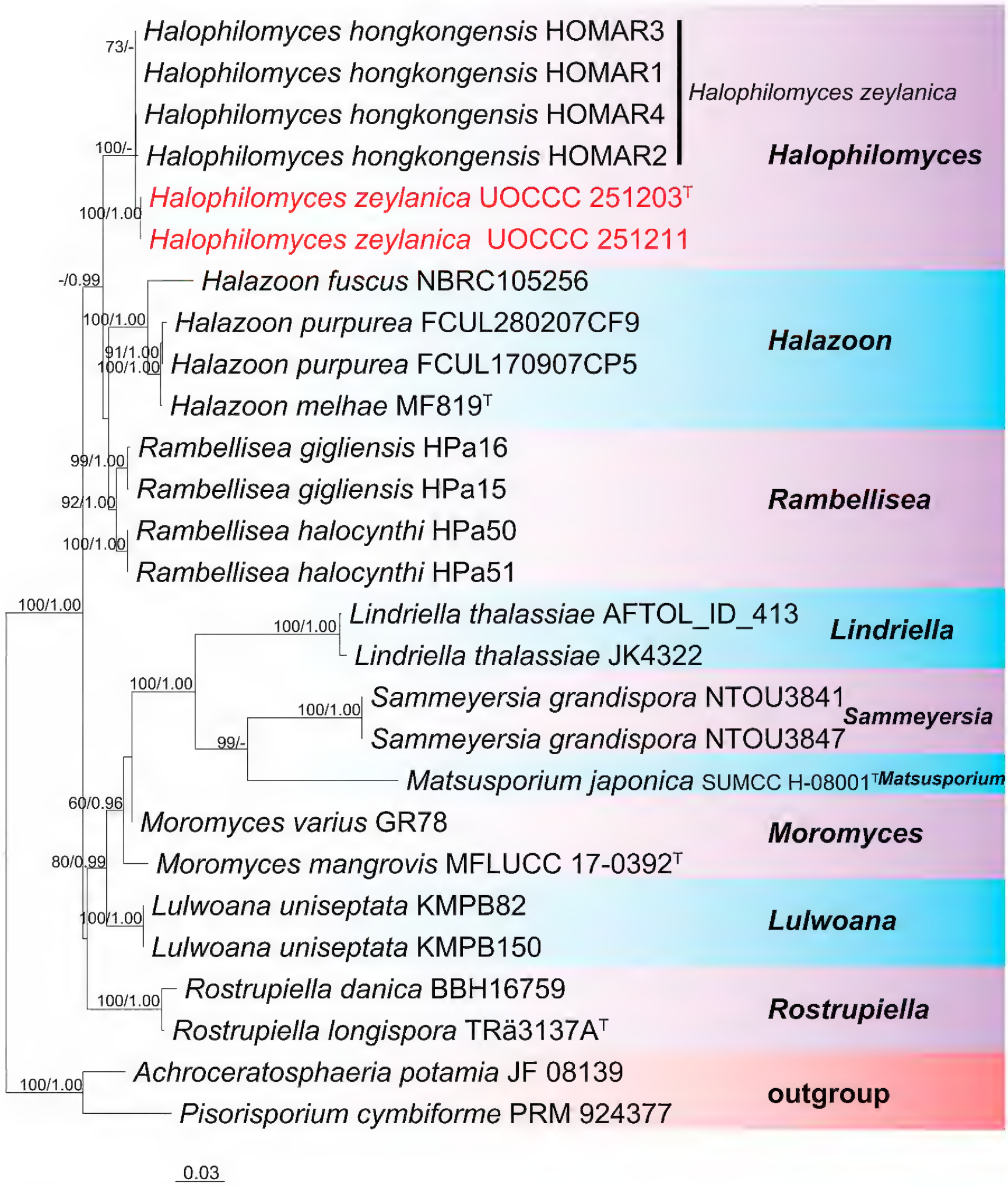

Figure 4. RAxML tree based on a combined dataset of partial ITS, LSU, and SSU DNA sequence analyses. Bootstrap support values for ML ≥ 60% and Bayesian posterior probabilities (BYPP) ≥ 0.9 are shown as ML/BI above the nodes. Type materials are indicated by the superscript "T" while newly generated sequences are shown in red.

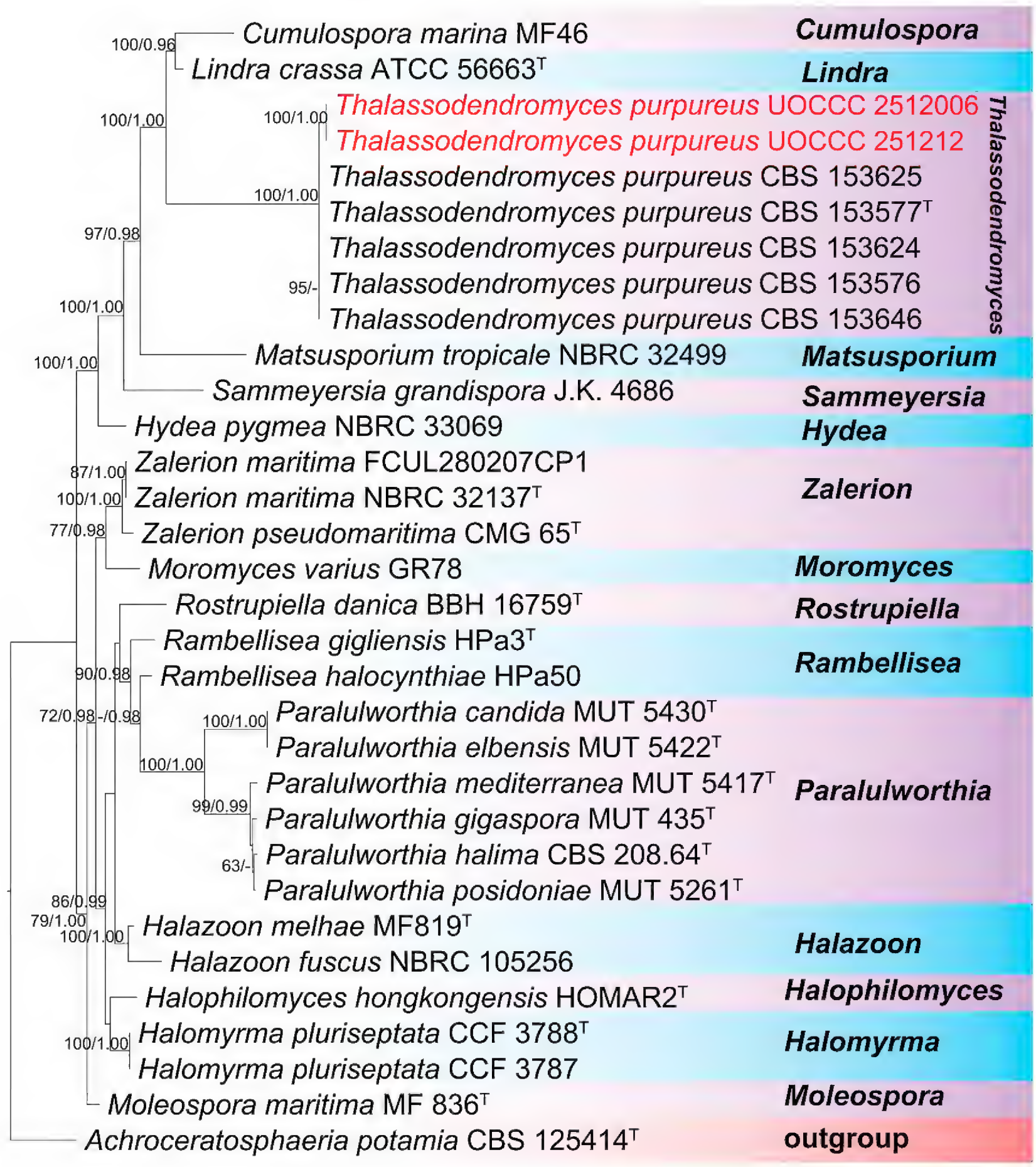

Figure 5. RAxML tree based on a combined dataset of partial ITS, LSU, and SSU DNA sequence analyses. Bootstrap support values for ML ≥ 60% and Bayesian posterior probabilities (BYPP) ≥ 0.9 are shown as ML/BI above the nodes. Type materials are indicated by the superscript "T" while newly generated sequences are shown in red.

***Neodevriesia saximollicula* D.S. Paiva, Fungal Systematics and Evolution 15: 66 (2024)**

Index Fungorum: IF852927

Fig. 6

Culture characteristics. Colonies on PDA velvety, irregular in shape, convex, reached 14–16 mm diam. after 14 days at 25 °C; grayish black center with black margin in forward view; reverse black. Colonies on *Enhalus acoroides*-infused PDA looked identical to those observed on PDA, with a slightly decreased radial growth, reaching 11–13 mm at 25 °C in 14 days of incubation.

Micromorphology. Hyphae 1.5–4 µm wide, heavily branched, septate, smooth, hyaline to olivaceous brown; no sporulation observed. Occasionally, thick-walled hyphal knots observed.

Material examined. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, living culture numbers, UOCCC 251201 = UOCCC 251209.

Notes. Paiva et al. (2025) introduced *Neodevriesia saximollicula* from stone artworks in Aveiro, Portugal. In their phylogenetic analyses (based on ITS and LSU), *Neodevriesia saximollicula* formed a separate, monophyletic clade within *Neodevriesia s. str.* In our phylogenetic analyses based on ITS, LSU, and *rpb*2 sequence data (Fig. 2), new strains UOCCC 251201 = UOCCC 251209 grouped with MUM 23.48 (ex-type) and PL127 of *Neodevriesia saximollicula* with high statistical support (100% ML and 1.00 BYPP in BI analyses, respectively). Hence, we identified UOCCC 251201 and UOCCC 251209 as *Neodevriesia saximollicula*.

To the best of our knowledge, this is the first report of *Neodevriesia saximollicula* from a marine or aquatic environment, specifically from the leaves of *Enhalus acoroides*. In addition, this is the first report of the genus *Neodevriesia* and *N. saximollicula* from Sri Lanka.

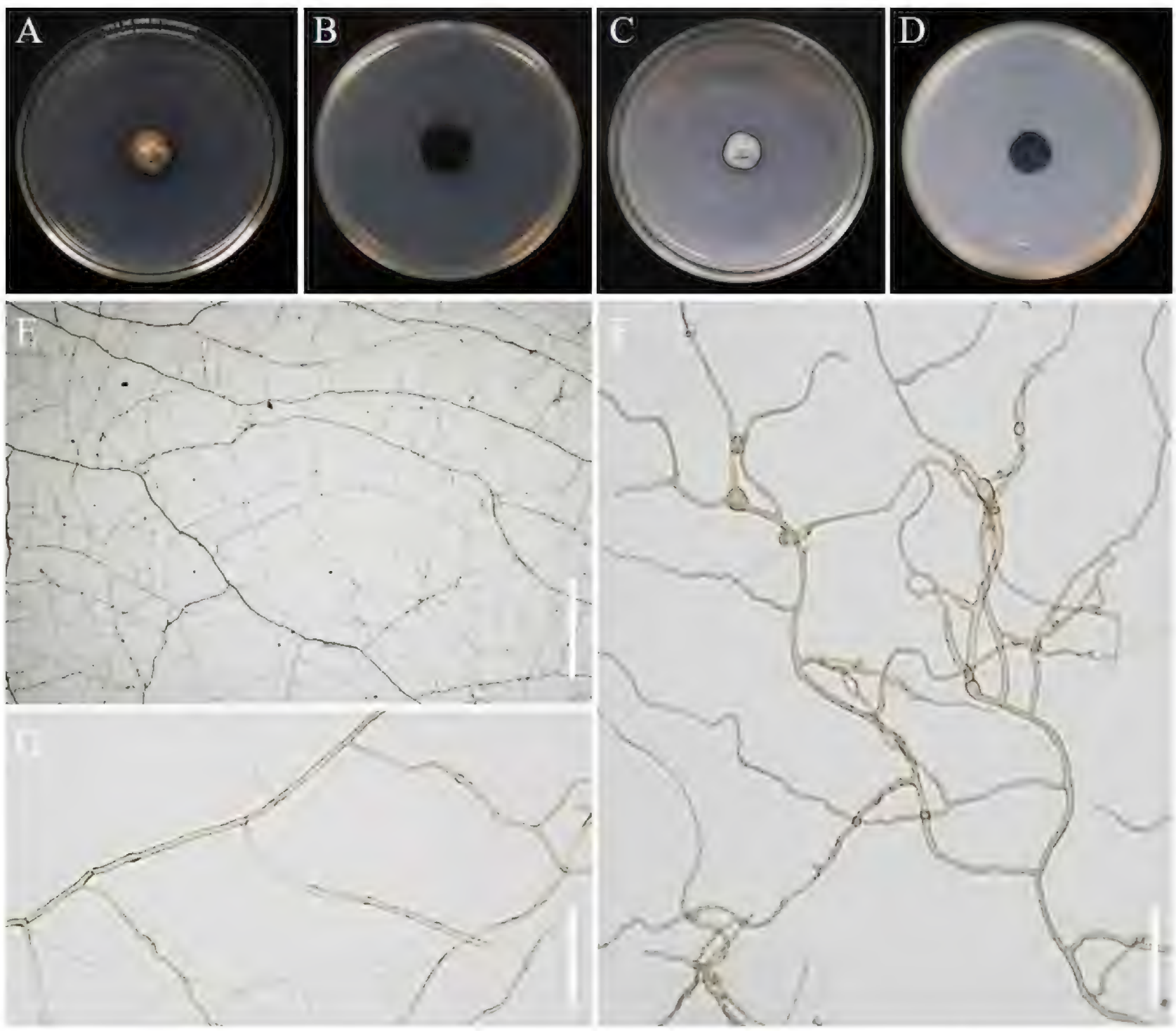

Figure 6. *Neodevriesia saximollicula* (UOCCC 251201 and UOCCC 251209). **A.** Forward and **B.** Reverse views of colony morphology of two-week-old cultures grown at 25 °C on PDA; **C.** Forward and **D.** Reverse views of 14-day-old cultures on seagrass-infused PDA; **E–G.** Heavily branched, septate hyphae. Scale bars: 50 µm (**E–G**).

***Neodevriesia zeylanica* Wijayaw., Rajakaruna, L.S. Han & K.G.S.U. Ariyaw., sp. nov.**

Index Fungorum: IF904758

Fig. 7

Etymology. The species epithet '*zeylanica*' refers to the old name of Sri Lanka, 'Ceylon.'

Culture characteristics. Colonies on PDA reached 6 diam. after 14 days at 25 °C, exhibiting extremely slow, uniform radial growth. Colonies were velvety with flat elevation, irregular outline, with undulate margin; grayish black in forward view, dark black in reverse. Colonies on *Enhalus acoroides*-infused PDA appeared identical to those on standard PDA.

Micromorphology. Hyphae septate, branched, initially pale brown, differentiating into dark brown, thick-walled moniliform chains composed of globose to ellipsoidal cells constricted at the septa, eventually forming heavily melanized intercalary chlamydospore-like cells in chains, 100–500 µm long, 2–5 µm thick; no conidia observed.

Typification. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, En71 (**holotype** RUSLH/247, dried culture; **ex-type** UOCCC 251202).

Additional material examined. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, En71, living culture, En71a = UOCCC 251210.

Notes. In the phylogenetic tree, the new isolates clustered with *Neodevriesia shakazului* (CPC 19782, ex-type) with high statistical support (92% ML and 0.99 BYPP in Bayesian analyses, respectively). Based on pairwise nucleotide comparisons, UOCCC 251202 and UOCCC 251210 diverged from *Neodevriesia shakazului* (CPC 19782, ex-type) by 19/533 bp (3.5%) in ITS and 15/827 bp (1.8%) in LSU. Our isolates failed to sporulate, except for some chlamydospore-like cells in linear chains. Although different techniques were used (see Materials and methods), we were unable to compare the microscopic morphological characteristics. Hence, based on the phylogenetic analyses (Fig. 2) and base pair differences, we introduce our isolates as a new species in *Neodevriesia s. str.*, namely *N. zeylanica*.

***Pleosporales* Luttr. ex M.E. Barr**

***Occultibambusaceae* D.Q. Dai & K.D. Hyde**

***Neooccultibambusa* Doilom & K.D. Hyde, Fungal Diversity 82: 126 (2016) [2017]**

Notes. The genus *Neooccultibambusa* was introduced by Doilom et al. (2017) from dead culms of *Bambusoideae* in Thailand, with a sexual morph (cylindrical to subcylindrical unitunicate asci and fusiform ascospores with 1–3 transverse septa) and chlamydospores forming in culture. Later, the genus was reported with hyphomycetous asexual morphs (Hyde et al. 2018). Currently, the genus comprises seven species and has been reported from China (Guizhou and Yunnan Provinces), Italy, and Thailand (Jayasiri et al. 2016; Hyde et al. 2018; Yu et al. 2021; Lu et al. 2025). In this study, we collected two

strains of *Neooccultibambusa* from *Enhalus acoroides*; multi-locus phylogenetic studies confirmed that these strains represent a novel species. Hence, we introduce *Neooccultibambusa zeylanica*.

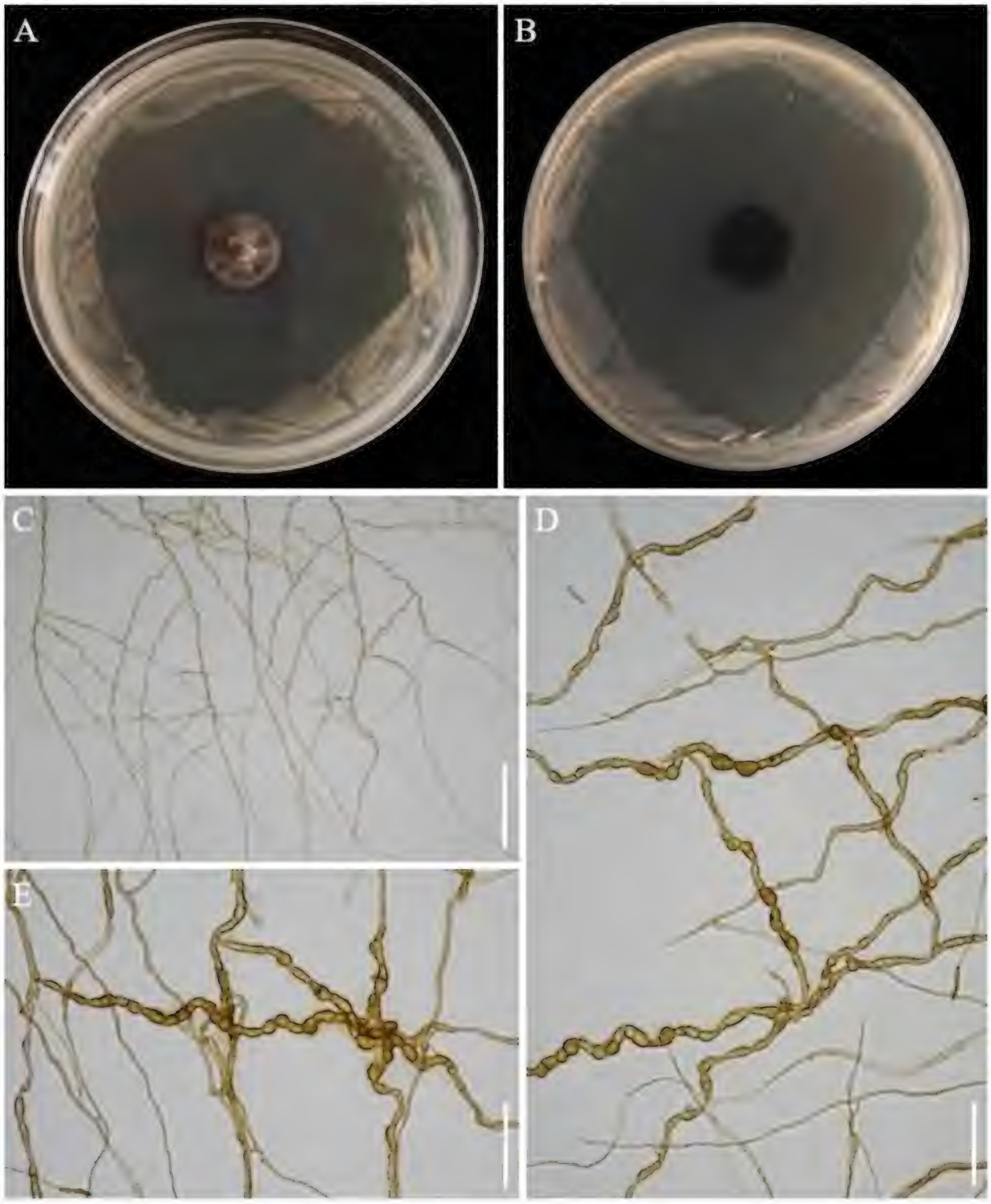

Figure 7. *Neodevriesia zeylanica* (UOCCC 251202 and UOCCC 251210). **A.** Forward and **B.** Reverse views of colony characteristics of two-week-old cultures grown at 25 °C on PDA; **C.** Sparsely branched, hyaline to pale brown hyphae; **D, E.** Irregularly branched, chlamydospore-like structures in chains. Scale bars: 50 µm (**C–E**).

Neooccultibambusa zeylanica **Wijayaw., Rajakaruna, L.S. Han & K.G.S.U. Ariyaw., sp. nov.**
Index Fungorum: IF904759
Fig. 8

Etymology. The species epithet '*zeylanica*' refers to the old name of Sri Lanka, 'Ceylon.'

Culture characteristics. Colonies on PDA velvety, circular with an undulate margin, raised, umbonate, attaining 16 mm diam. after 14 days at 25 °C; surface grey at center, white toward margin; reverse black. Colonies on *Enhalus acoroides*-infused PDA are similar.

Micromorphology. Hyphae 1–2 µm wide, profusely branched, septate, smooth-walled, with globose to subglobose or irregular, intercalary, chlamydospore-like structures, 5–30 × 2–5 µm ($\bar{x}$ = 18 × 3.5 µm diam., n = 30), smooth-walled cells, hyaline to olivaceous.

Typification. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, En 42 (**holotype** RUSLH/248, dried culture; **ex-type** UOCCC 251207).

Additional material examined. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic of healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, En 42, living culture En 42a = UOCCC 251213; *Ibid*., living culture En 54a = En 54.

Notes. Our new strains of *Neooccultibambusa* are accommodated within *Neooccultibambusa s. str.* as a separate clade (Fig. 3), thus introducing *Neooccultibambusa zeylanica* sp. nov. here. *Neooccultibambusa zeylanica* cultures failed to produce any defined microscopic spore-like structures in culture, although different techniques were used for sporulation. Hence, we could not compare its morphological characteristics with those of other members of the genus. Therefore, the introduction of this novel taxon is based solely on molecular differences between the ex-type of the new species and its closely related species.

Sordariomycetes **O.E. Erikss. & Winka**
Lulworthiales **Kohlm., Spatafora & Volkm.-Kohlm.**
Lulworthiaceae **Kohlm., Spatafora & Volkm.-Kohlm.**

Halophilomyces **Xiao Wang, L. Pecoraro & H.B. Liu ex Wijayaw. & P.M. Kirk**
Index Fungorum: IF904724

= *Halophilomyces* Xiao Wang, L. Pecoraro & H.B. Liu, J. Fungi 10 (7, no. 474): 10 (2024) (Nom. Inval. Art. 40.7); Index Fungorum Registration Identifier IF854689.

Type species. *Halophilomyces zeylanica* Wijayaw., Rajakaruna, D.J. Bhat, P.M. Kirk & K.G.S.U. Ariyaw., sp. nov.

Endophytic on seagrass species *Halophila ovalis* and *Enhalus acoroides*. Hyphae with abundant loop-like structures. Chlamydospores in basipetal chains. Conidia generally increasing in size from base to apex. Solitary conidia present,

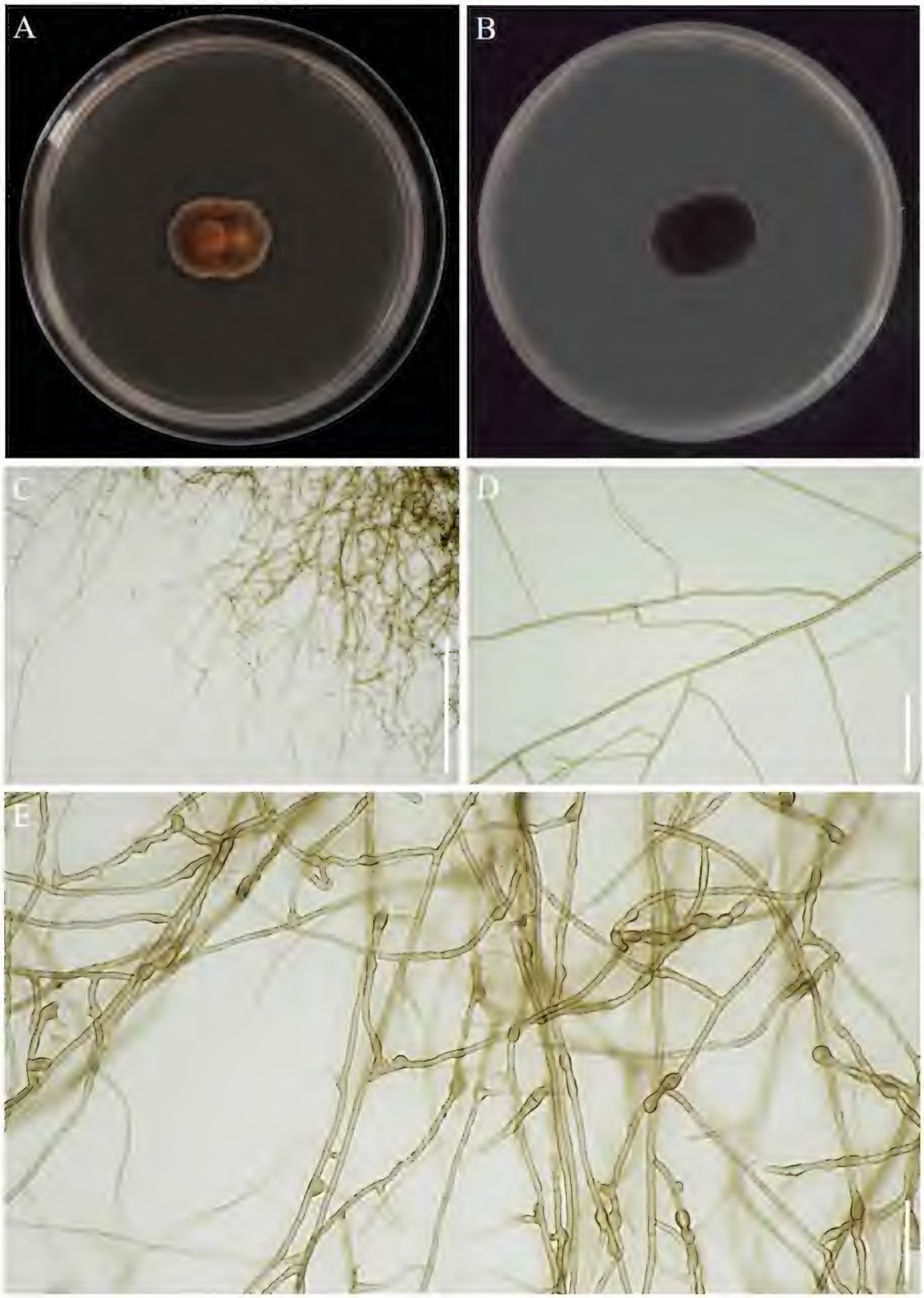

Figure 8. *Neooccultibambusa zeylanica* (UOCCC 251207 and UOCCC 251213). **A.** Forward and **B.** Reverse views of colony morphology of two-week-old cultures grown at 25 °C on PDA; **C.** Microscopic features observed from 14-day-old cultures illustrating loosely interwoven, sparsely branched, hyaline to pale brown hyphae; **D.** Long, thin, septate hyphae; **E.** Irregularly branched, septate hyphae with chlamydospore-like cells with thickened, smooth cell walls. Scale bars: 100 µm (**C**); 50 µm (**D, E**).

1–4-septate, deeply constricted at septa, coiled to spiral, dark brown, smooth-walled (Wang et al. 2024; this study).

Notes. Wang et al. (2024) introduced *Halophilomyces* (type species: *H. hongkongensis*) from the roots and rhizomes of *Halophila ovalis* (*Hydrocharitaceae*), a seagrass species in Hong Kong, China. However, *H. hongkongensis* (the type species of *Halophilomyces*) is invalid (Art. 40.7 (Shenzhen)); thus, the genus is correspondingly invalid.

In this study, we isolated *H. hongkongensis* from healthy leaves of *Enhalus acoroides*. Morphologically, the new isolates resemble the original description (as in Wang et al. 2024) and phylogenetically reside in the same clade as *H. hongkongensis* (Fig. 4).

Halophilomyces zeylanica **Wijayaw., Rajakaruna, D.J. Bhat, P.M. Kirk & K.G.S.U. Ariyaw., sp. nov.**

Index Fungorum: IF904723

Fig. 9

= *Halophilomyces hongkongensis* Xiao Wang, L. Pecoraro & H.B. Liu, J. Fungi 10 (7, no. 474): 10 (2024) (Nom. inval., Art. 40.7 (Shenzhen)); Index Fungorum Registration Identifier IF854690.

Etymology. The species epithet '*zeylanica*' refers to the old name of Sri Lanka, 'Ceylon.'

Culture characteristics. Surface cottony, filamentous, round in shape with raised margin. Colonies cultured on PDA reaching 52–55 mm diam. at 25 °C after 14 days, forming dense areal mycelium with partly submerged hyphae, white to olive at center; white at edges in forward view; reverse black with white margin.

Micromorphology. Mycelium partly superficial, partly immersed, composed of 3.3–3.9 µm wide, septate, branched, pale brown to olivaceous brown, smooth hyphae, with abundant hyphal loops. Conidiophores reduced to conidiogenous cells. Conidiogenous cells micronematous to semi-macronematous, holoblastic. Conidia acrogenous, solitary to catenate, 1–4-septate, deeply constricted at septa, coiled to spiral when in chains, dark brown, smooth-walled, 24–54 µm diam. ($\bar{x}$ = 32.2 diam., n = 30), globose to subglobose, with apical cell 14–25 µm, basal cell 9–22 µm. Single-celled conidia 9–30 µm diam. ($\bar{x}$ = 22.1 µm diam., n = 30), present, rarely found; Chlamydospores in chains, 5–8-celled, intercalary in hyphae, with cells ellipsoidal to globose, 14–21 µm diam., olivaceous brown, smooth.

Typification. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara (**holotype** RUSLH/249, dried culture; **ex-type** UOCCC 251203).

Additional material examined. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy leaves of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, living culture EN 39a = UOCCC 251211.

Notes. Phylogenetically, the new collections (UOCCC 251203 and UOCCC 251211) formed a sister clade with *Halophilomyces hongkongensis*

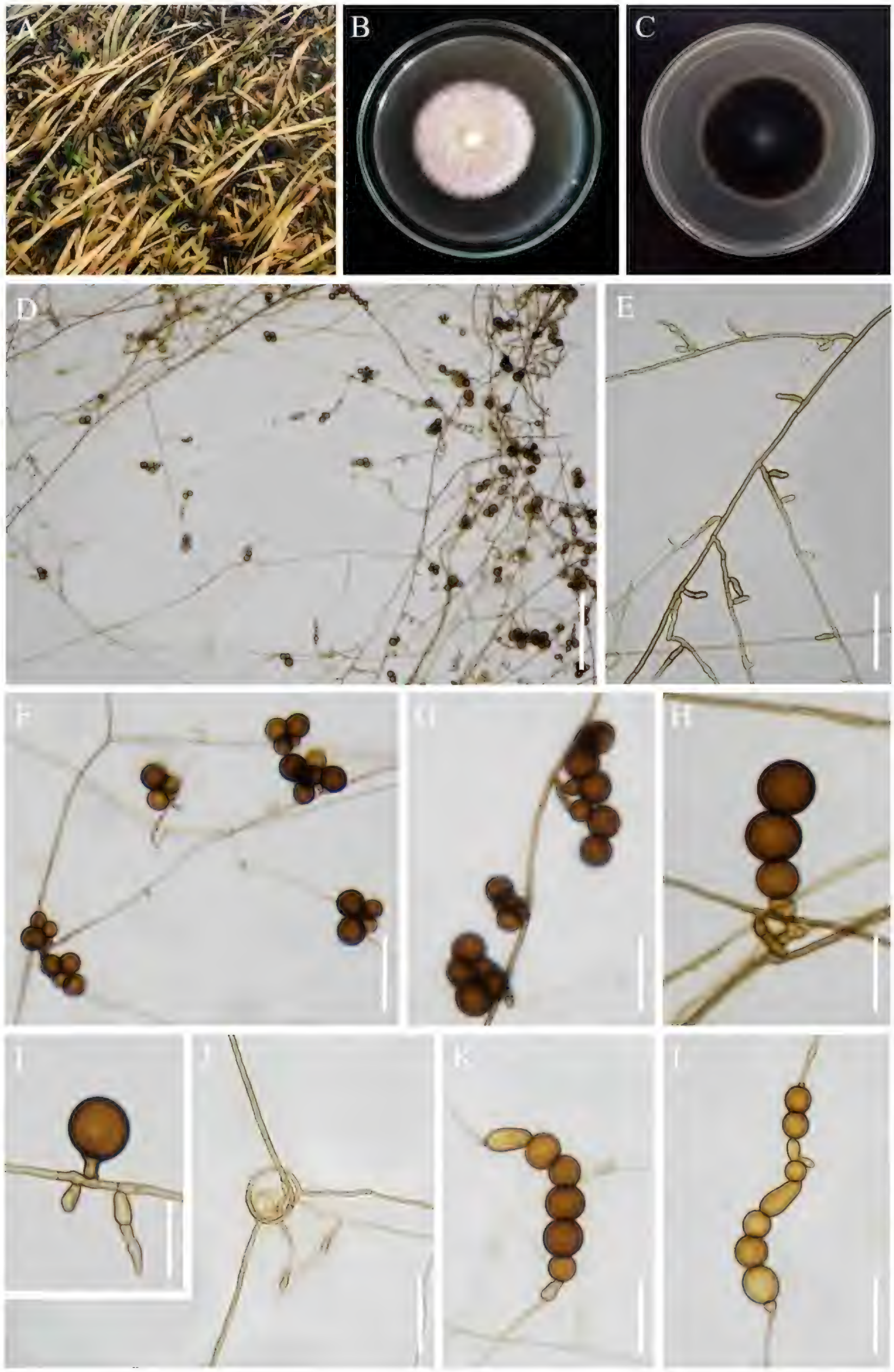

Figure 9. *Halophilomyces zeylanica* (UOCCC 251203 and UOCCC 251211). **A.** Submerged leaf canopy of *Enhalus acoroides*; **B.** Forward; **C.** Reverse views of colony morphology of two-week-old cultures grown at 25 °C on PDA; **D.** Overall view of the mycelia; **E.** Branched, septate hyphae; **F–H.** Multicellular mature conidia; **I.** Single-cell mature conidia; **J.** Loop structures formed by the hyphae; **K, L.** Multicellular chlamydospores. Scale bars: 50 μm (**C–K**).

(HOMAR1, HOMAR2, HOMAR3, and HOMAR4) with 100% ML support. The new isolates have only four base pair differences in the ITS locus compared to the ex-type of *H. hongkongensis* and no differences in the LSU and SSU loci. Conidial dimensions of the new collections resemble those described in Wang et al. (2024). Hence, we confirm that our new strains belong to *Halophilomyces hongkongensis* (Fig. 4).

Wang et al. (2024), in the original publication that introduced *Halophilomyces* and *H. hongkongensis*, did not designate a holotype for the type species; thus, both the type species and the genus are invalid (Art. 40.1 (Index Fungorum 2025). Here, we designate our new collection (the dried culture) as the new holotype RUSLH/249 and deposit a new living culture (UOCCC 251203) as the ex-type. Thus, we validate the genus with a new Index Fungorum Registration Identifier and provide a new name for *Halophilomyces hongkongensis*, namely *Halophilomyces zeylanica*, with a new Index Fungorum Registration Identifier.

***Thalassodendromyces* Vohník & Réblová, IMA Fungus 16 (e157688): 22 (2025)**

Notes. Réblová et al. (2025) introduced *Thalassodendromyces purpureus* (the type species of *Thalassodendromyces*) from surface-sterilized roots of the seagrass *Thalassodendron ciliatum* from Mauritius.

***Thalassodendromyces purpureus* Vohník & Réblová, IMA Fungus 16 (e157688): 22 (2025)**

Index Fungorum: IF858635

Fig. 10

Culture characteristics. Filamentous, flat, filiform in margin, with colonies on seawater-supplemented PDA attaining 60–63 mm diam. after 14 days at 25 °C, with no growth observed on *Enhalus acoroides* extract-amended PDA or standard PDA after 30 days at 25 °C (three replicates), partly superficial and partly submerged, olivaceous brown center, lighter at the edges in forward view; reverse olivaceous with lighter margin.

Micromorphology. Hyphae 5–6 µm wide, septate, smooth, olivaceous to brown, chlamydospores in chains, cells ellipsoidal, brown in color. The length of the chlamydospores varies between 13–30 × 7–14 µm ($\bar{x}$ = 21.2 × 10.8 µm, n = 10).

Material examined. SRI LANKA • North Western Province, Puttalam District, Kalpitiya, Puttalam Lagoon, endophytic in healthy rhizomes of *Enhalus acoroides*, 23 August 2023, O. Rajakaruna & S. Udagedara, living cultures, En13 = UOCCC 251206, UOCCC 251212.

Notes. Our new strains (UOCCC 2512006 and UOCCC 251212) cluster with the ex-type of *Thalassodendromyces purpureus* (CBS 153577) and other putative strains with high statistical support (Fig. 5). In the original description, Réblová et al. (2025) did not observe chlamydospores or any other microscopic characteristics. However, our newly isolated strains produced chlamydospores in chains on seawater-supplemented PDA, but no growth was observed on standard PDA.

To our knowledge, this is the first report of *Thalassodendromyces purpureus* from *Enhalus acoroides* and the first record of both the genus and species from Sri Lanka.

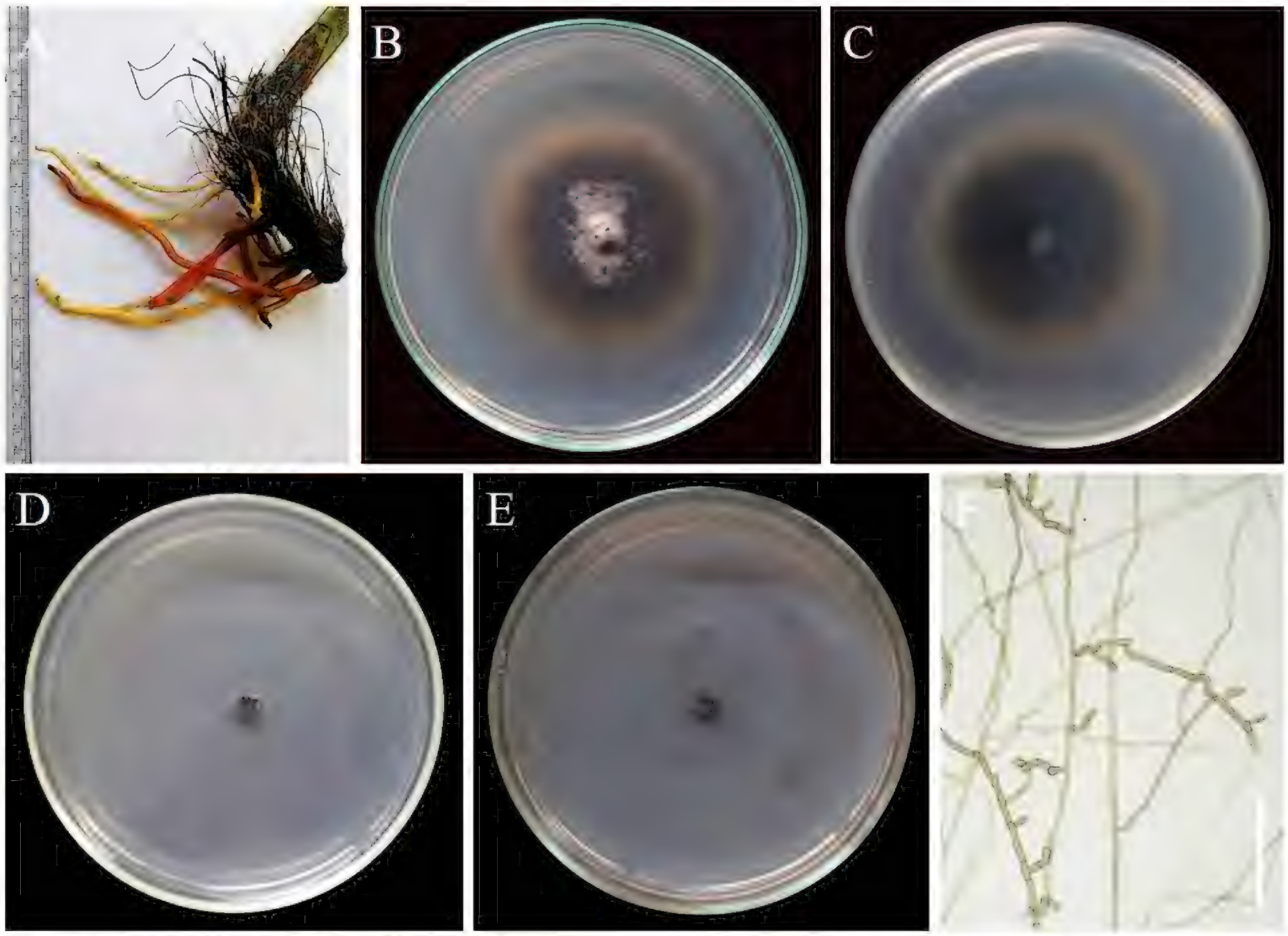

Figure 10. *Thalassodendromyces purpureus* (UOCCC 251206 and UOCCC 251212). **A.** Rhizome of *Enhalus acoroides*; **B.** Forward; **C.** Reverse views of colony morphology of two-week-old cultures at 25 °C on seawater-supplemented PDA; **D, E.** Two-week-old colonies on seagrass-infused PDA showing no growth; **F.** Branched, septate hyphae; **G, H.** Young chlamydospores in chains; **I.** Mature chlamydospores in chains. Scale bars: 50 µm (**F–I**).

Discussion

Seagrasses are a group of flowering plants that have fully adapted to a submerged lifestyle and are reported from shallow marine waters (Hemminga and Duarte 2000; Larkum et al. 2006, 2018). They have been reported as monospecific or multispecific meadows and spread over a larger surface area, covering the seabed (Duarte 2001; Short et al. 2016). The mycobiome associated with different seagrass species has been explored in different studies (e.g., Ettinger and Eisen 2019; Hurtado-McCormick et al. 2019), but further studies based on modern screening techniques (such as high-throughput sequencing) are essential to understand fungal diversity, particularly from biodiversity-rich, understudied regions such as the Sri Lankan seas (Rajakaruna et al. 2024).

Sri Lanka is a biodiversity-rich country, yet its marine fungal diversity remains poorly documented (Wijayawardene et al. 2023). In this study, we selected *Enhalus acoroides*, a common seagrass species in the Kalpitiya Lagoon, Puttalam District, Sri Lanka, to recover culturable filamentous fungi. In total, ten different endophytic strains were isolated from healthy leaves, roots, and rhizomes using the surface sterilization method.

Four strains were identified as members of *Neodevriesia s. str.*, and multilocus phylogenetic analyses confirmed that they represent two different species. *Neodevriesia saximollicula* was identified as a first report from *Enhalus acoroides* in Sri Lanka. Originally, *Neodevriesia saximollicula* was reported from a terrestrial habitat; therefore, this is the first report of this species from a marine habitat. *Neodevriesia zeylanica* was introduced to accommodate two other strains of *Neodevriesia s. str.*, which formed a distinct clade in the phylogenetic analyses. Previously, four members of *Neodevriesia s. str.*, viz., *N. aestuarina* (from Ria de Aveiro in Portugal *fide* Crous et al. 2020), *N. grateloupiae* (from marine algae in China *fide* Wang et al. 2017), and *N. manglicola* Devadatha et al. (from mangroves *fide* Yuan et al. 2020), were isolated from marine environments. Herein, we report two more species of *Neodevriesia* (i.e., *Neodevriesia saximollicula* and *N. zeylanica*) from marine habitats, of which *N. zeylanica* is new to science. Furthermore, this is the first report of the genus *Neodevriesia* from Sri Lanka.

In this study, we also introduce a new member of *Neooccultibambusa s. str.*, i.e., *N. zeylanica*, from *Enhalus acoroides* in Sri Lanka. Members of *Neooccultibambusa* have been predominantly reported from terrestrial habitats (e.g., Doilom et al. 2017; Lu et al. 2025). Hence, this is the first report of a member of this genus from an aquatic habitat, particularly from a marine environment. Moreover, this is the first report of the genus from *Enhalus acoroides* (thus a new host record) and a new record from Sri Lanka (a new geographical record).

The genus *Halophilomyces* was introduced by Wang et al. (2024) with *Halophilomyces hongkongensis* as the type species. We isolated two strains of *Halophilomyces hongkongensis* in this study, and both strains were phylogenetically and morphologically confirmed. However, Wang et al. (2024) did not designate a type specimen for *Halophilomyces hongkongensis*; therefore, the species remained invalid. The generic name is also regarded as invalid because its type species is invalid (Index Fungorum 2025). Since the new strains are identical to *Halophilomyces hongkongensis*, we designated the dried

culture as the holotype and provided a new name, *H. zeylanica*. Consequently, *H. hongkongensis* becomes a synonym of *H. zeylanica*. The new name was registered in Index Fungorum and obtained a new identifier. Since the type species is validly published here, the genus also becomes valid. We registered the name *Halophilomyces* Xiao Wang, L.Pecoraro & H.B.Liu ex Wijayaw. & P.M.Kirk in Index Fungorum and obtained a new identifier.

In this study, we isolated *Thalassodendromyces purpureus* (the type species of *Thalassodendromyces fide* Réblová et al. 2025) from *Enhalus acoroides* in Sri Lanka. The genus is monotypic and has only been reported from the roots of the seagrass *Thalassodendron ciliatum* in Mauritius. As far as we know, this is the first report of *Thalassodendromyces purpureus* from *Enhalus acoroides* (a new host record) and from Sri Lanka (a new country record).

This study confirms that the underexplored Sri Lankan marine habitats are rich in fungal diversity. All the species we isolated were slow growers and thus highly susceptible to contamination by common fungal epiphytes (such as *Aspergillus* spp. and *Penicillium* spp.) and bacteria. Hence, future studies should be planned using highly selective media (Réblová et al. 2025). Furthermore, it is necessary to focus on identifying unculturable fungi from the mycobiome of seagrasses in understudied regions such as Sri Lanka.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Data curation: O.R., S.U., L.S.H., K.G.S.U.A., M.K.W., N.N.W.; Funding acquisition: T.C.B., N.N.W., D.J.B., T.M.D., D.D.Q.; Project administration: N.N.W., K.G.S.U.A.; Writing – original draft: O.R., S.U., N.N.W., L.S.H., M.K.W., W.W., S.H.; Writing – review and editing: N.N.W., D.D.Q., K.G.S.U.A., S.H., P.M.K., F.Y., D.J.B.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Al-Samarrai TH, Schmid J (2000) A simple method for extraction of fungal genomic DNA. Letters in Applied Microbiology 30(1): 53–56. https://doi.org/10.1046/j.1472-765x.2000.00664.x

Capella-Gutiérrez S, Silla-Martınez JM, Gabaldón T (2009) trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics (Oxford, England) 25: 1972–1973. https://doi.org/10.1093/bioinformatics/btp348

Crous PW, Wingfield MJ, Chooi YH, Gilchrist CLM, Lacey E, Pitt JI, Roets F, Swart WJ, Cano-Lira JF, Valenzuela-Lopez N, Hubka V, Shivas RG, Stchigel AM, Holdom DG, Jurjević Ž, Kachalkin AV, Lebel T, Lock C, Martín MP, Tan YP, Tomashevskaya MA, Vitelli JS, Baseia IG, Bhatt VK, Brandrud TE, De Souza JT, Dima B, Lacey HJ, Lombard L, Johnston PR, Morte A, Papp V, Rodríguez A, Rodríguez-Andrade E, Semwal KC, Tegart L, Abad ZG, Akulov A, Alvarado P, Alves A, Andrade JP, Arenas F, Asenjo C, Ballarà J, Barrett MD, Berná LM, Berraf-Tebbal A, Bianchinotti MV, Bransgrove K, Burgess TI, Carmo FS, Chávez R, Čmoková A, Dearnaley JDW, Santiago ALCM de A, Freitas-Neto JF, Denman S, Douglas B, Dovana F, Eichmeier A, Esteve-Raventós F, Farid A, Fedosova AG, Ferisin G, Ferreira RJ, Ferrer A, Figueiredo CN, Figueiredo YF, Reinoso-Fuentealba CG, Garrido-Benavent I, Cañete-Gibas CF, Gil-Durán C, Glushakova AM, Gonçalves MFM, González M, Gorczak M, Gorton C, Guard FE, Guarnizo AL, Guarro J, Gutiérrez M, Hamal P, Hien LT, Hocking AD, Houbraken J, Hunter GC, Inácio CA, Jourdan M, Kapitonov VI, Kelly L, Khanh TN, Kisło K, Kiss L, Kiyashko A, Kolařík M, Kruse J, Kubátová A,

Kučera V, Kučerová I, Kušan I, Lee HB, Levicán G, Lewis A, Liem NV, Liimatainen K, Lim HJ, Lyons MN, Maciá-Vicente JG, Magaña-Dueñas V, Mahiques R, Malysheva EF, Marbach PAS, Marinho P, Matočec N, McTaggart AR, Mešić A, Morin L, Muñoz-Mohedano JM, Navarro-Ródenas A, Nicolli CP, Oliveira RL, Otsing E, Ovrebo CL, Pankratov TA, Paños A, Paz-Conde A, Pérez-Sierra A, Phosri C, Pintos Á, Pošta A, Prencipe S, Rubio E, Saitta A, Sales LS, Sanhueza L, Shuttleworth LA, Smith J, Smith ME, Spadaro D, Spetik M, Sochor M, Sochorová Z, Sousa JO, Suwannasai N, Tedersoo L, Thanh HM, Thao LD, Tkalčec Z, Vaghefi N, Venzhik AS, Verbeken A, Vizzini A, Voyron S, Wainhouse M, Whalley AJS, Wrzosek M, Zapata M, Zeil-Rolfe I, Groenewald JZ (2020) Fungal Planet description sheets: 1042–1111. Persoonia: Molecular Phylogeny and Evolution of Fungi 44: 301. https://doi.org/10.3767/persoonia.2020.44.11

Devarajan PT, Suryanarayanan TS, Geetha V (2002) Endophytic fungi associated with the tropical seagrass *Halophila ovalis* (*Hydrocharitaceae*). Indian Journal of Geo-Marine Sciences 31: 73–74.

Doilom M, Dissanayake AJ, Wanasinghe DN, Boonmee S, Liu JK, Bhat DJ, Taylor JE, Bahkali AH, McKenzie EH, Hyde KD (2017) Microfungi on *Tectona grandis* (teak) in Northern Thailand. Fungal Diversity 82(1): 107–182. https://doi.org/10.1007/s13225-016-0368-7

Doilom M, Dissanayake AJ, Wanasinghe DN, Boonmee S, Liu JK, Bhat DJ, Taylor JE, Bahkali AH, McKenzie EHC, Hyde KD (2017) Microfungi on *Tectona grandis* (teak) in northern Thailand. Fungal Diversity 82: 107–182. https://doi.org/10.1007/s13225-016-0368-7

Duarte CM (2001) Seagrasses. In Encyclopedia of Biodiversity, 2nd ed.; Academic Press, Cambridge. https://doi.org/10.1016/b0-12-226865-2/00241-8

Ettinger CL, Eisen JA (2019) Characterization of the mycobiome of the seagrass, *Zostera marina*, reveals putative associations with marine chytrids. Frontiers in Microbiology 10: 2476. https://doi.org/10.3389/fmicb.2019.02476

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—Application to the identification of mycorrhizae and rusts. Molecular Ecology 2(2): 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Gostinčar C, Stajich JE, Gunde-Cimerman N (2023) Extremophilic and extremotolerant fungi. Current Biology 33(14): R752–R756. https://doi.org/10.1016/j.cub.2023.06.011

Hall T (2004) BioEdit. Ibis Therapeutics, Carlsbad, CA, 92008, USA. http://www.mbio.ncsu.edu/BioEdit/bioedit.html [Accessed 18 March 2005]

Hemminga MA, Duarte CM (2000) Seagrass Ecology, 1st ed. Cambridge University Press, Cambridge.

Hendricks KE, Christman MC, Roberts PD (2017) A Statistical Evaluation of Methods of In-Vitro Growth Assessment for *Phyllosticta citricarpa*: Average Colony Diameter vs. Area. PLOS ONE 12(1): e0170755. https://doi.org/10.1371/journal.pone.0170755

Hurtado-McCormick V, Kahlke T, Petrou K, Jeffries T, Ralph PJ, Seymour JR (2019) Regional and Microenvironmental Scale Characterization of the *Zostera muelleri* Seagrass Microbiome. Frontiers in Microbiology 10: 1011. https://doi.org/10.3389/fmicb.2019.01011

Hyde KD, Chaiwan N, Norphanphoun C, Boonmee S, Camporesi E, Chethana KWT, Dayarathne MC, de Silva NI, Dissanayake AJ, Ekanayaka AH, Hongsanan S, Huang SK, Jayasiri SC, Jayawardena RS, Jiang HB, Karunarathna A, Lin CG, Liu JK, Liu NG, Lu YZ, Luo ZL, Maharachchimbura SSN, Manawasinghe IS, Pem D, Perera RH, Phukhamsakda C, Samarakoon MC, Senwanna C, Shang QJ, Tennakoon DS, Thambugala KM, Tibpromma S, Wanasinghe DN, Xiao YP, Yang J, Zeng XY, Zhang JF, Zhang SN,

Bulgakov TS, Bhat DJ, Cheewangkoon R, Goh TK, Jones EBG, Kang JC, Jeewon R, Liu ZY, Lumyong S, Kuo CH, McKenzie EHC, Wen TC, Yan JY, Zhao Q (2018) Mycosphere notes 169–224. Mycosphere: Journal of Fungal Biology 9(2): 271–430. https://doi.org/10.5943/mycosphere/9/2/8

Index Fungorum (2025) Published on the Internet, The Royal Botanic Gardens, Kew. http://www.indexfungorum.org [Accessed 25 February 2026]

Jayasiri SC, Hyde KD, Jeewon R, Bhat JD, Camporesi E, Kang JC (2016) *Neooccultibambusa jonesii*, a novel taxon within *Occultibambusaceae*. Mycosphere: Journal of Fungal Biology 7(9): 1458–1472. https://doi.org/10.5943/mycosphere/7/9/17

Jones EBG, Pang KL, Abdel-Wahab MA, Scholz B, Hyde KD, Boekhout T, Ebel R, Rateb ME, Henderson L, Sakayaroj J, Suetrong S, Dayarathne MC, Kumar V, Raghukumar S, Sridhar KR, Bahkali AHA, Gleason FH, Norphanphoun C (2019) An online resource for marine fungi. Fungal Diversity 96: 347–433. https://doi.org/10.1007/s13225-019-00426-5

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Larkum AWD, Orth RJ, Duarte CM (2006) Seagrasses: Biology, Ecology and Conservation, 1st ed. Springer, Dordrecht, The Netherlands.

Larkum AWD, Kendrick GA, Ralph PJ (2018) Seagrasses of Australia: Structure, Ecology and Conservation, 2nd ed. Springer, Cham. https://doi.org/10.1007/978-3-319-71354-0

Lu L, Karunarathna SC, Rajeshkumar KC, Elgorban AM, Jayawardena RS, Hongsanan S, Suwannarach N, Kumla J, Xiong YR, Hyde KD, Han MY (2025) Unveiling fungal diversity associated with coffee trees in China using a polyphasic approach and a global review of coffee saprobic fungi. IMA Fungus 16: e144874. https://doi.org/10.3897/imafungus.16.144874

Ma X (2016) Study on complete mitochondrial genome of *Cypridopsis vidua* and molecular phylogeny of Ostracoda. East China Normal University, Shanghai, China.

Paiva DS, Fernandes L, Pereira E, Mesquita N, Tiago I, Trovão J, Portugal A (2025) Unearthing limestone fungal diversity: Description of seven novel species from Portugal Fungal Systematics and Evolution 15: 47–77. https://doi.org/10.3114/fuse.2025.15.02

Panno L, Bruno M, Voyron S, Anastasi A, Gnavi G, Miserere L, Varese GC (2013) Diversity, ecological role and potential biotechnological applications of marine fungi associated to the seagrass *Posidonia oceanica*. New Biotechnology 30(6): 685–694. https://doi.org/10.1016/j.nbt.2013.01.010

Quaedvlieg WG, Binder M, Groenewald JZ, Summerell BA, Carnegie AJ, Burgess TI, Crous PW (2014) Introducing the consolidated species concept to resolve species in the *Teratosphaeriaceae*. Persoonia-Molecular Phylogeny and Evolution of Fungi. 33(1): 1–40. https://doi.org/10.3767/003158514X681981

Rajakaruna O, Wijayawardene NN, Udagedara S, Jayasinghe PK, Gunasekara SS, Boonyuen N, Bamunuarachchige TC, Ariyawansa KG (2024) Exploring fungal diversity in seagrass ecosystems for pharmaceutical and ecological insights. Journal of Fungi (Basel, Switzerland) 10(9): 627. https://doi.org/10.3390/jof10090627

Rambaut A (2012) FigTree v1.4.0.a Graphical viewer of phylogenetic trees. http://tree.bio.ed.ac.uk/software/figtree/ [Accessed 3 January 2023]

Réblová M, Nekvindová J, Hynar O, Vohník M (2025) From seagrass roots to saline soils: discovery of two new genera in *Lulworthiales* (*Sordariomycetes*) from osmotically

stressed habitats. IMA Fungus 12(16): e157688. https://doi.org/10.3897/imafungus.16.157688

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Senanayake IC, Rathnayaka AR, Marasinghe DS, Calabon MS, Gentekaki E, Lee HB, Hurdeal VG, Pem D, Dissanayake LS, Wijesinghe SN, Bundhun D (2020) Morphological approaches in studying fungi: Collection, examination, isolation, sporulation and preservation. Mycosphere: Journal of Fungal Biology 11(1): 2678–2754. https://doi.org/10.5943/mycosphere/11/1/20

Short FT, Short CA, Novak AB (2016) Seagrasses. The Wetland Book. Springer, Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-007-6173-5_262-1

Species Fungorum (2025) Published on the Internet, The Royal Botanic Gardens, Kew. http://www.speciesfungorum.org [Accessed 25 February 2026]

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and postanalysis of large phylogenies. Bioinformatics (Oxford, England) 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the ML web servers. Systematic Biology 57: 758–771. https://doi.org/10.1080/10635150802429642

Vaidya G, Lohman DJ, Meier R (2011) Sequence Matrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics: The International Journal of the Willi Hennig Society 27: 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

Venkatachalam A, Thirunavukkarasu N, Suryanarayanan TS (2015) Distribution and diversity of endophytes in seagrasses. Fungal Ecology 13: 60–65. https://doi.org/10.1016/j.funeco.2014.07.003

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8): 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Wang MM, Shenoy BD, Li W, Cai L (2017) Molecular phylogeny of *Neodevriesia*, with two new species and several new combinations. Mycologia 109(6): 965–974. https://doi.org/10.1080/00275514.2017.1415075

Wang X, Pecoraro L, Chen J, Tang Y, Lee S, Chen S, Liu H (2024) *Halophilomyces hongkongensis*, a novel species and genus in the *Lulworthiaceae* with antibacterial potential, colonizing the roots and rhizomes of the seagrass *Halophila ovalis*. Journal of Fungi (Basel, Switzerland) 10: 474. https://doi.org/10.3390/jof10070474

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: A guide to methods and applications. Academic Press, San Diego, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wijayawardene NN, Dai D-Q, Jayasinghe PK, Gunasekara SS, Nagano Y, Tibpromma S, Suwannarach N, Boonyuen N (2022) Ecological and Oceanographic Perspectives in Future Marine Fungal Taxonomy. Journal of Fungi (Basel, Switzerland) 8: 1141. https://doi.org/10.3390/jof8111141

Wijayawardene NN, Dai DQ, Premarathne BM, Wimalasena MK, Jayalal RU, Wickramanayake KD, Dangalla H, Jayathunga WH, Brahmanage RS, Karunarathna SC, Weerakoon G (2023) Checklist, typification details, and nomenclature status of

ascomycetous fungi originally described in Sri Lanka. Phytotaxa 611(1): 1–105. https://doi.org/10.11646/phytotaxa.611.1.1

Yu XD, Zhang SN, Cheewangkoon R, Liu JK (2021) Additions to *Occultibambusaceae* (*Pleosporales*, *Dothideomycetes*): Unrevealing palmicolous fungi in China. Diversity 13(11): 516. https://doi.org/10.3390/d13110516

Yuan HS, Lu X, Dai YC, Hyde KD, Kan YH, Kušan I, He SH, Liu NG, Sarma VV, Zhao CL, Cui BK (2020) Fungal diversity notes 1277–1386: Taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 104(1): 1–266.

Supplementary material 1

Single-gene tree for *Neodevriesia*

Authors: Nalin N. Wijayawardene, Oshadi Rajakaruna, Li-Su Han, Madhara K. Wimalasena, Thushara C. Bamunuarachchige, Jayarama D. Bhat, Turki M. Dawoud, Susantha Udagedara, Wannapawn Watsuntorn, Sinang Hongsanan, Paul M. Kirk, Fuqiang Yu, Dong-Qin Dai, Kahandawa G. S. U. Ariyawansa

Data type: jpg

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Link: https://doi.org/10.3897/mycokeys.129.184555.suppl1

Supplementary material 2

Single-gene tree for *Neooccultibambusa*

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Data type: jpg

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